THE
AMERICAN NATURALIST

VOL. XLIX. *October, 1915* No. 586

EARLY PORTRAYALS OF THE OPOSSUM

DR. CHARLES R. EASTMAN
AMERICAN MUSEUM OF NATURAL HISTORY

THE quaint animal figures found in olden time works on natural history are interesting not only as bearing upon the contemporary state of zoological science and the art of book-making, but also because many of the illustrations belong to a regular sequence or lineage which can be traced back, like the textual descriptions, to primitive sources. To a certain extent this has already been done, or at least indicated, in the work by John Ashton, entitled "Curious Creatures of Zoology."

A subject deserving of the attention of naturalists but which appears to have been neglected, is an historical and systematic investigation of animal figures introduced in early American cartography. Thanks to the magnificent facsimile reproductions of sixteenth century maps which have been published during recent years in this country and abroad, abundant materials for this purpose are now easily accessible. As for the "relaciones" of early voyagers and travelers in the western world, very few of these have been published with scientific commentaries, and among the really important seventeenth century writers on Central and South American natural history, only the works of Hernandez (1628) and Marcgrav[1] (1648) have been systematically annotated. The first letter

[1] See the commentaries on these authors by Lichtenstein and Martius, 1827 and 1853, in the publications of the Berlin and Bavarian Academies of Science.

written from the newly discovered world, by Dr. Chanca, companion of Columbus, was not adequately edited and annotated until after four centuries had passed. Vespucci's letters also are deserving of mention in this connection.[2]

In view of the fact that several communications have appeared in *Nature* during the past year concerning the first mention of the opossum in literature, it may not be inopportune to trace the pedigree of some of the early illustrations of this animal, both in maps and in printed works. At the same time a few of the older printed descriptions of American marsupials may be noticed. And we will observe first of all that the earliest reference to the common American opossum is found in the famous collection of voyages published in 1504 by Angelo Trivigiano, under the caption of "Libretto de Tutta la Navigatione de Re de Spagna, de le Isole et Terreni Novamente Trovati." In Chapter XXX of that work it is mentioned that a live specimen, taken by the Pinzons in Brazil in 1500, was exhibited in Granada.

In Decas II of Peter Martyr's "De Nove Orbe," published in 1511, occurs the first published description of the American tapir; and immediately following this the opossum is referred to in these words:

> There is also an animal which lives in the trees, feeds upon fruits, and carries its young in a pouch in the belly; no writer as far as I know has seen it, but I have already sufficiently described it in the Decade which has already reached Your Holiness before your elevation, as it was then stolen from me to be printed.

In 1547 and 1548, and again from 1549 to 1555, Hans Stade of Homburg, Hesse, passed some time in Brazil, and wrote or dictated an account of his strange adventures, which was published at Marburg in 1557. Under the caption of "Servoy," Chapter XXXII, we read:

[2] See Fernandez de Ybarra in *Journ. Amer. Med. Assoc.* for September, 1906, and in Misc. Coll. Smithson. Inst. for the same year. Vespucci's first letter (1497) was republished in facsimile by Varnhagen in 1893, having for frontispiece a design by Stradanus dating from about 1580, in which various South American animals are well represented. Mention occurs in this letter of the iguana, puma and ocelot from the coast of Tampico.

There is also a kind of game, called *servoy,* which is as large as a cat, and has a tail like a cat; its fur is gray, and sometimes grayish black. And when it breeds, it bears five or six young. It has a slit in the belly about half a span in length. Within the slit there is yet

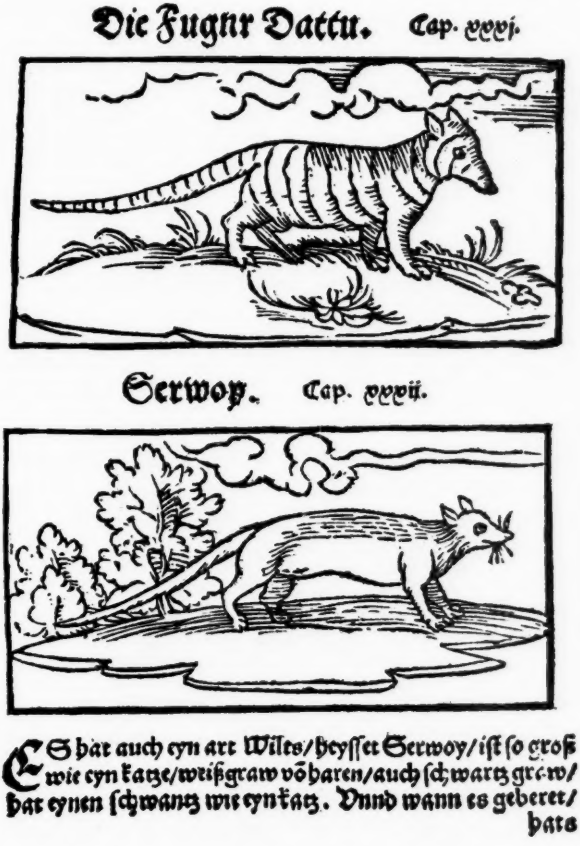

Die Fugnr Dattu. Cap. xxxj.
Serwoy. Cap. xxxij.
Es hat auch eyn art Wilts/heysset Serwoy/ist so gros
wie eyn katze/wißgraw vōharen/auch schwartz gre-w/
hat eynen schwantz wie eyn katz. Vnnd wann es geberet/
hats

FIG. 1. The "Dattu" (tatou or armadillo) and "Servoy" (opossum); after Hans Stade, 1557.

another skin; for its belly is not open, and within this slit are the teats. Wherever it goes, it carries its young in the pocket between the two skins. I have often helped to catch them and have taken the young ones from out of the slit.

In the original edition of the work just quoted woodcuts are given of both the opossum and armadillo (*Dasypus novemcinctus* Linn.) and these are reproduced in the present article (Fig. 1) from a copy belonging to the New York Public Library. The armadillo is thus described in Stade's "Wahrhaftig Historia":

> There is another sort of animal found in this country which the savages call *dattu;* it stands about six inches high and is nine inches long; its body is covered all over, except underneath, with a kind of armor. This covering is horn-like, and the plates overlap one another like those of chain armor. This animal has a very long snout, and is usually found on rocks. It feeds on ants. Its flesh is sweet and I have often eaten of it.

Two works published at about the same time as the narrative of Stade also contain mention of the opossum, the name of "Simivulpa" or Fox-ape and "Su" being

FIG. 2. The "Simivulpa" (*Didelphis*); after Sebastian Münster, 1558.

applied to the creature. In the Italian edition (1558) of Sebastian Münster's "Cosmographia" occurs this passage, accompanied by an illustration which we have reproduced in Fig. 2:

Trovasi in quel luogo [Brazil] un animal prodigioso, le cui parti davanti si rassomigliano a volpe & quella di dietro à Simia mai suoi piedi sono como di huomo, ha le orecchi di civetta, & sotto le ventre como una borsa, nella quale tien nascosti suoi figliuoli, finche crescono di sorte che possino caminare securamente da lor stesi, & procurarsi il cibo senza tutela della madre, ne mai escono di quella borsa se non quando lattano. Quest' animale mostruosa con tre suoi figliuoli fu portato in Sibilía & indi in Granatá."—p. 1187.

Münster's illustration of the "Simivulpa" is evidently derived from figures of the opossum appearing in several editions of Ptolemy's "Geography" from 1522 onward,

FIG. 3. Earliest known figure of the opossum; from the Waldseemüller world-map of 1516.

and other early maps of South America, all traceable in the first instance to Waldseemüller's world-map of 1516, where the same representation occurs (Fig. 3). It is there accompanied by essentially the same legend as one finds in the "*Tabula Terre nove*" of the 1522 Ptolemy, and in later maps and atlases,[3] such as Cornelius de Jode's (1585), and van Linschoten's (1598).

[3] Modern reproductions of South American maps showing these figures may be seen in Winsor's "Narrative and Critical History of America," and in the magnificent collection published by the Brazilian government under the direction of Baron de Rio Branca. The representation of a Brazilian landscape in the Cantino map of 1500, shown in our Fig. 4, is from a photograph of Harrisse's colored reproduction.

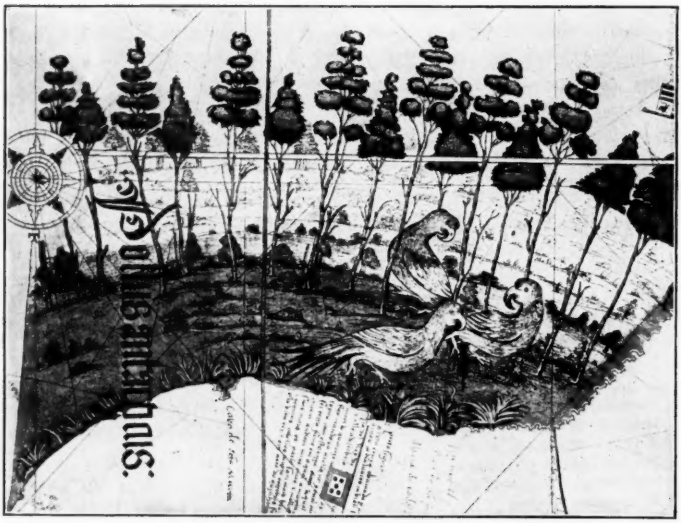


FIG. 4. One of the earliest representations of an American landscape; from the Cantino map of 1500.

André Thevet, who sojourned for a short time in Brazil, published his "Singularitez de la France Antarctique" in 1558. His description of the "Su," in reality the opossum, is paraphrased by Conrad Gesner, Edward Topsell, J. E. Nieremberg and John Jonston under that caption, and his grotesque caricature of the beast is reproduced by these authors. It is also introduced in sixteenth century cartography of the two Americas. Blaeu, in his world-map of 1605, places the "Su" and its descriptive legend in the region of Nova Francia;[4] and in the La Plata region of the same map occurs still another figure of the opossum, based upon the century-old drawing which appears in the Waldseemüller world-map. Our Fig. 5 is taken from Thevet, and Fig. 6 from Nieremberg, whose "Historia Naturæ" was published in 1635.

In Wolfe's English edition of van Linschoten's "Voyages," figures of the sloth and "Simivulpa" are intro-

[4] See the new facsimile edition (1914) published by Dr. E. L. Stevenson under the auspices of the Hispanic Society of America.

FIG. 5. The "Su" (common opossum); after André Thevet, 1555.

FIG. 6. The "Flaquatzin" (wooly opossum); from Topsell, after Nieremberg, 1635.

duced in the Brazilian and Argentine region of the map of the South American continent, and at page 232 of this work occurs the following description of one of these beasts:

There is likewise another wonderful and strange beast of Gesnerus called a Foxe ape, on the belly whereof Nature hath formed an other belly, wherein when it goeth into any place, it hideth her young ones, and so beareth them about with her. This beast hath a body and members like a foxe, feete like mens hands, or like sea cattes feete, eares like a batte. It is never seene that this beast letteth her young ones come forth but when they sucke, or ease themselves, but are alwayes therein, until they can gette their own meate.

Passing now to the seventeenth century writers, we find this account of *Didelphis* in Raphe Hamor's "True Discourse of the Present Estate of Virginia" (London, 1615):

For true it is, that the Land is stored with plenty and variety of wild beastes, Lions, Bears, Deere of all sorts. . . . Beavers, Otters, Foxes, Racounes, almost as big as a Fox, as good meat as a lamb, Hares, wild Cats, Muske rats, Squirrels flying, and other of three or foure sorts, Apossumes, of the bignesse and likenesse of a Pigge, of a moneth ould, a beast of as strange as incredible nature; she hath commonly seauen young ones, sometimes more and sometimes lesse, which she taketh vp into her belly, and putteth forth againe without hurt to her selfe or them.

Of each of these beasts, the Lion excepted, my selfe have many times eaten, and can testifie that they are not only tastefull, but also wholesome and nourishing foode.

FIG. 7. The opossum and young; after César de Rochefort, 1658.

About the same time Captain John Smith wrote the following brief characterization of the opossum, in his "Description of Virginia" (1612):

An opossum hath a head like a Swine, and a taile like a Rat, and is of the bignesse of a Cat. Under her belly she hath a bag, wherein she lodgeth, carrieth, and suckleth her young.

After Nieremberg, a Jesuit professor at Madrid, whose work on natural history (1635) is chiefly a compilation, we come to George Marcgrav and Wilhelm Piso; and

their contributions on Brazilian natural history, published in 1648, are recognized as highly meritorious.

Ulysses Aldrovandi's large posthumous folio on Quadrupeds (1637, p. 103) also contains a figure of the opossum (otherwise interpreted, however) which is clearly traceable to the early cartographic designs. But it is unnecessary to pursue the subject further, except to state that Fig. 7 is copied after Charles César de Rochefort's engraving of an opossum ("Histoire des Îles Antilles," 1658), and Fig. 8 shows the same animal, acording to Eduard Seler's interpretation, as depicted in one of the Maya Codices (Nuttall, 71).

FIG. 8. Maya representation of the opossum (?) From Eduard Seler, after Nuttall Codex, 71.

Among other mammalian figures in pre-Columbian Maya and Mexican colored drawings[5] that have been preserved are several that represent a spotted dog, probably one of the varieties of "Alcos" mentioned by Hernandez. The occurrence of an indigenous spotted dog in Central America is of interest in view of the fact that a similar race is depicted in ancient Egyptian, Assyrian and Pelasgian animal effigies and paintings, some of the figures dating as far back as about 3000 B.C.

The oldest known representations of the hunting dog of the ancient Egyptians, together with a number of large African mammals, are inscribed in a palette discovered a few years ago at Hierakonpolis.

[5] See Edward Seler, "Die Tierbilder der mexicanischen und Maya-Handschriften," *Zeitschr. f. Ethnol.*, Jhrg. 41, 1909. A. M. Tozzer and G. M. Allen, "Animal Figures in the Maya Codices," papers of Peabody Museum Arch. Ethnol., Vol. 4, No. 3, 1910. References to the literature on ancient Egyptian and Assyrian animal effigies will be found in *Amer. Journ. Philol.*, Vol. XXX, 1909, pp. 322–331. The early history of the rhinoceros is traced by B. Laufer in Publication 179 of the Field Museum, and medieval ideas of the elephant are portrayed by E. D. Cuming in a recent number of *Field* (April 3, 1915).

Concerning the several varieties of ancient Inca or Ancon dog that are known from well-preserved Peruvian mummies, Nehring[6] is of the opinion that their remote ancestry is traceable to the North American wolf (*Lupus occidentalis* var. *mexicanus* and *rufus*). The great antiquity of domesticated dogs in South America is indicated also by a canine skull which R. Lydekker has described from the superficial deposits of Buenos Aires. This dog, according to Dr. Lydekker,[7] "though apparently contemporaneous with many of the wonderful extinct mammals of the Pampas, yet shows unmistakable signs of affinity with domesticated breeds, although the precise relationship has not been established."

Reference having already been made to animal figures in early American cartography, we may call attention in closing this sketch to a memoir by Aníbal Cardoso in the *Anales* of the Buenos Aires Museum for 1912 (Vol. XV), on the origin of Argentine horses.[8] The writer endeavors to show from historical evidence that large numbers of horses existed in the interior of the country prior to the Spanish Conquest, and a figure of one of these animals drawn by Sebastian Cabot in his world-map of 1544 is interpreted as indicating that wild herds were seen by that navigator in 1531. A portion of Cabot's map is reproduced in Señor Cardoso's memoir (p. 379), and also in one by J. T. Medina on the voyage of Sebastian Cabot.

Nevertheless the conclusion appears unavoidable that, had the horse actually persisted in the western hemisphere down to the time of the advent of Europeans, some traces of it would certainly appear in the culture of the primitive inhabitants.

[6] *Sitzungsber. ges Naturf. Freunde*, Berlin, 1884.

[7] R. Lydekker, "Mostly Mammals," London, 1903, p. 204.

[8] "Antigüedad del Caballo en el Plata." On the horse in post-conquistorial times in North America see Clark Wissler, "The Influence of the Horse in the Development of Plains Culture," in *Amer. Anthropol.*, Vol. XVI, 1914.

SEVENTEEN YEARS SELECTION OF A CHARACTER SHOWING SEX-LINKED MENDELIAN INHERITANCE[1]

RAYMOND PEARL

I

In 1898 there was begun at the Maine Agricultural Experiment Station an experiment in breeding Barred Plymouth Rock fowls, having for its purpose the improvement by selection of the character winter egg production. This investigation has continued to the present time. A résumé of the results to date, considered with reference to their bearing upon the general biological problem of selection, may be of some interest.

The experiment has fallen into three divisions or periods: viz., (1) the period from 1898 to 1907, (2) the period from 1908 to 1912, and finally (3) the period from 1912 to date. Detailed reports on the methods of breeding in operation have been published elsewhere.[2] For purposes of clear orientation in the present discussion it will be well here briefly to review the facts as to the methods of breeding used in each of the periods. With these facts definitely in mind we may then proceed to an examination of the results.

1. *The Period from 1898 to 1907.*—During this period the breeding followed the plan outlined at the beginning by Woods and Gowell. Essentially it consisted of the following elements.

1. Trap-nest record of the performance of each individual female.
2. Selection as breeders of all females which laid more than a definite number of eggs (150) in the first laying year.

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 87.

[2] Cf. particularly Woods, C. D., and Gowell, G. M., U. S. Dept. Agr. Bur. Anim. Ind. Bulletin 90, 1906, pp. 42; Pearl, R., and Surface, F. M., *Ibid.* Bulletin 110, Part I, 1909, pp. 80; Pearl, Me. Agr. Expt. Stat. Ann. Rept., 1911, pp. 113–176; and Pearl, *Jour. Exp. Zool.*, Vol. 13, 1912, pp. 153–268

3. Selection as breeders of males whose dams had laid more than another definite number of eggs (200).
4. The indiscriminate mass breeding, *without* individual pedigrees, of all individuals selected as described under 2 and 3, and, in consequence,
5. *No test of the progeny* of particular matings with respect to their laying ability.

This may be designated as the *period of mass selection.*

The following statement regarding the methods used in this period was made by Woods and Gowell (*loc. cit.*, p. 8):

> The plans followed in this breeding work are based upon everyday, practical common sense, and are the same as would be used in building up a high-producing strain of dairy animals. Individual records of performance are kept. The large producers are mated with sons of large producers in the hope of obtaining a race of improved layers. In the first year's work three birds laid over 200 eggs each, and this fact led to the adoption of that number of eggs as the minimum performance for a "registered" bird. Other than this there was no reason for selecting 200 as the number of eggs necessary to entitle a bird to registration. Any other number, as 190 or 210, might have been taken with equal propriety, just as horsemen might have selected some other time than 2.30 by which to determine a standard horse.

2. *The Period from 1908 to 1912.*—For reasons which have been fully set forth elsewhere[3] it was decided not to continue the breeding along the same plan after 1907. The new plant, put into operation first in the breeding season of 1908, was calculated primarily to furnish definite information regarding the mode of inheritance of the character winter egg production. It involved essentially the following items:

1. Trap-nest record of the performance of each individual female.
2. The selection of both males and females was made on a *double* basis, including in addition to the individual's own performance as in the earlier plan, also the idea of progeny performance. In practice this worked out *for hens* in the following way: Plans were made to see whether there could

[3] Pearl and Surface, *loc. cit.*

be formed by selection and propagated three distinct strains of winter egg producers, namely, high, mediocre and low. This involved, *on the individual performance side,* the separate selection in the first years of *three* classes of females as breeders: (*a*) good winter producers, with records before March 1 of above 30 eggs; (*b*) mediocre winter producers, with records below 30 eggs; and (*c*) poor winter producers, which laid no eggs before March 1. The division at 30 eggs was, after the first year, merely a nominal one in the selection of *high* producers. Actually only birds were used in the *a* class whose records materially exceeded 30 eggs, running up to over 100 eggs in some cases.

The *progeny performance* idea was carried out in two ways in the breeding. In the first place, no female was selected for the *high* winter production breeding pens, for example, unless, in addition to her own high winter record, all her sisters and her dam were high producers. In the second place, of all females fulfilling the above qualification only those were bred a second time whose progeny from the first year's mating had proven to be all high producers. Similar types of selection were followed by the mediocre and low lines, except that segregating families were put in the mediocre class.

3. The selection of males was along essentially the same lines, with only such difference as is involved in the fact that the male makes no performance record himself. Males were put into the breeding pen the first time on the basis of the records of their dams, on the one hand, and of their sisters, on the other hand. Those whose progeny proved that they were transmitting the character to which selection was being made were used a second or even third time as breeders.
4. Complete individual pedigrees, whereby each off-

spring individual's parentage, both male and female, was known.

5. The records of production of the progeny of each mating separately recorded and studied as a unit.

It will be noted that there are but two essential differences between the plan in this period and that followed in the earlier one. These are: first and most important, that in this second period the principle of *progeny testing* was introduced into the scheme of breeding. The second difference was that selection was carried on for low production as well as for high, which had not been previously done. A third difference is apparently found in the fact that in this second period of selection the winter record rather than the yearly record is made the basis of selection. This is in no way an essential difference. The reasons for adopting the winter period have been set forth in detail elsewhere[4] and need not be repeated. It suffices to say here that essentially the same results and conclusions will be reached if one uses winter production or annual production.

As a result of the studies made in this period on the plan of breeding outlined the mode of inheritance of the character winter production was definitely determined, and has been confirmed by subsequent work.[5] The character was shown to be Mendelian in its genetic behavior, depending upon two factors, one of which is sex-linked.

3. *The Period from 1912 to Date.*—The only difference in the mode of breeding the stock of Barred Plymouth Rocks in this period, as compared with the preceding one, is found in the fact that during this last period *all selections for low and mediocre production have been dropped.* The breeding for high production alone continues, with only such differences in the details of manipulation of the breeding stock as would naturally follow a definite knowledge of the mode of inheritance of the character,

[4] Pearl, 1912, *loc. cit.*, and Me. Agr. Exp. Stat. Ann. Rept., 1914, pp. 217–236. Cf. also Wilson and Murphy, *Jour. Dept. Agr. Ireland*, Vol. XIV, No. 2.

[5] Pearl, 1912, *loc. cit.*, also AMER. NAT., Vol. XLIX, 1915, pp. 306–317, and Curtis and Pearl, *Jour. Exp. Zoology*, Vol. 19, 1915, pp. 45–59.

and of the gametic constitution of particular individuals with reference to that character. As a matter of fact, all low-producing lines were dropped at the end of the laying year 1911–12. Certain of the mediocre lines were continued a year longer. In the laying flock of 1913–14 there were no birds which had been bred for anything other than high production, so far as the breeder's deliberate intention went.

II

The results of this seventeen year selection period are set forth in Table I.

TABLE I

MEAN WINTER PRODUCTION PER BIRD OF THE BARRED PLYMOUTH ROCK FLOCKS FROM 1899 TO 1915

Laying Year	Mean Winter Production of All Birds	No. of Birds Making Winter Records	Mean Winter Production of All Birds Selected for *High* Production	Mean Winter Production of All Birds Selected for *Low* Production
1899–1900	41.03 eggs	70	—	—
1900–1901	37.88 "	85	—	—
1901–1902	45.23 "	48	—	—
1902–1903	26.01 "	147	—	—
1903–1904	26.55 "	254	—	—
1904–1905	35.04 "	515	—	—
1905–1906	40.65 "	635	—	—
1906–1907	22.44 "	653	—	—
1907–1908	19.93 "	780	—	—
1908–1909	26 69 "	359	54.16	22.06
1909–1910	31.76 "	247	47.57	25.05
1910–1911	30.49 "	264	50.58	17.00
1911–1912	35.93 "	232	57.42	16.43
1912–1913	43.01 "	182	52.61	—
1913–1914	52.20 "	192	52.20	—
1914–1915	45.89 "	179	45.89	—
Totals and means	35.05 "	4,842	51.49	20.14

The data of this table are shown graphically in Fig. 1.

From the table and diagrams the following results appear:

1. The number of individuals involved in this experiment, on each one of which exact trap-nest records have been kept, is large, amounting nearly to five thousand. This number is large enough to lead to conclusions which are trustworthy. It will be shown presently that wherever it has been possible to compare the results on egg produc-

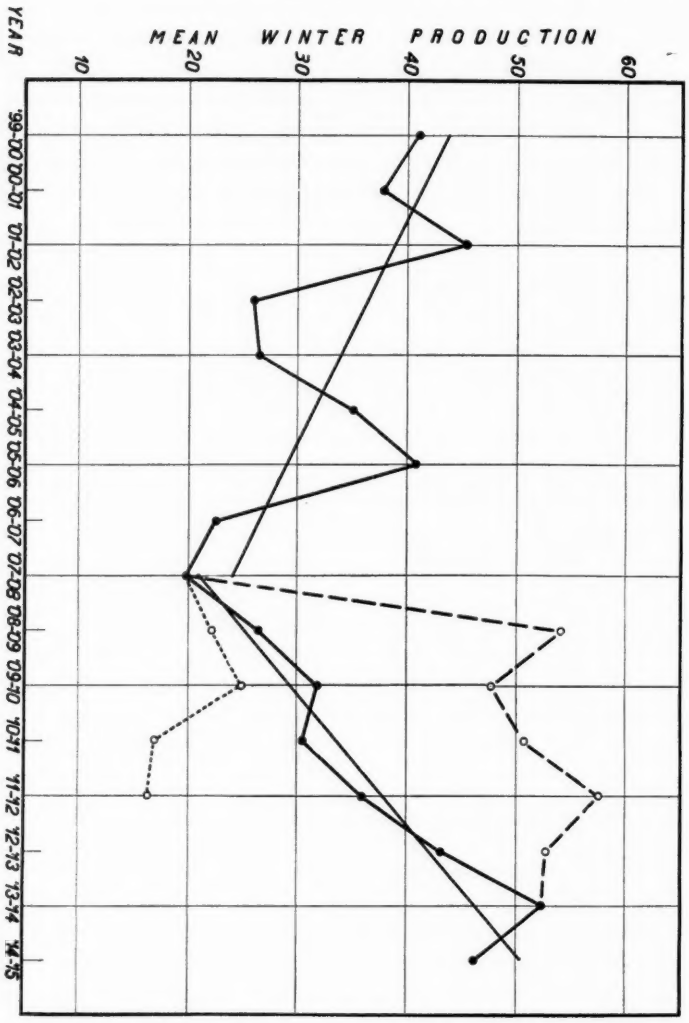


FIG. 1. Graph showing the course of mean winter egg production between the years 1899 and 1915. The solid lines and circles give the total flock means. The two straight lines, fitted by the method of least squares to the observed flock means, have the equations, $y = 43.655 - 2.181x$, and $y = 17.070 + 4.148x$. The open circles and broken (dash) line give the means of the lines selected for high winter production between the years 1908 and 1915. The dotted line and open circles give the mean winter production of the lines selected for low production between the years 1908 and 1912.

tion obtained in this experiment with independently determined norms the general trustworthiness and normality of the present data have been demonstrated.

2. From the beginning of the experiment through the laying year 1907–08 the general trend of mean production was downward, with minor fluctuations from year to year. In other words during the period in which the system of breeding was mass selection for high production without progeny test there was no change of the mean in the direction of the selection. The fluctuations in mean production during this period were, in the main, due probably to two sets of causes: (*a*) environmental differences in different years acting at one point or another in the life history of the birds; (*b*) random fluctuations in the genetic constitution of the male birds used as breeders in successive years, brought about because of the ignorance of the breeder, in the absence of any individual progeny testing plan, of the ability of any particular male to transmit high fecundity to his daughters. The first of these factors needs no special discussion and is relatively of minor importance. The second will be dealt with in detail farther on in the paper.

3. Since the laying year 1907–08 there has been a steady increase in mean winter production for the whole flock, except for the years 1910–11 and 1914–15. In the former year the decline in the mean is slight, and is probably due to unfavorable environmental influences. In 1914–15 the decline is certainly due to such causes. In the hatching season of 1914 an inexperienced man was in charge of the incubation and rearing. He had very poor success, and the Barred Plymouth Rock pullets available for the laying houses in the fall were relatively few in number, of a relatively late average date of hatching, and poorly grown. It is remarkable, not that the mean winter production was lower in 1914–15 than in 1913–14, but rather that it was so high as it was, taking all the circumstances into account. It appears that the system of breeding which made the selections on a progeny test basis was immediately and, to date, continuously effective.

4. That selection on a progeny test basis was effective is demonstrated not only by the general flock averages, but also by the fact that it was possible to propagate separately high and low producing strains. The high producing strains differed widely from the low producing in mean winter production. Taking the average for seven years in the case of the high, and four years in the case of the low, it appears that the mean winter production of the high producing strains was approximately two and a half times that of the low producing strains. At the end of the laying year 1911–12 the low producing lines were dropped. In the next year (breeding season of 1913) no birds were bred which were known to belong to segregating lines. Of course some were included which proved afterwards to have been segregating, but this fact could not, in any such case, have been told in advance from the records in hand. The propagation of low producing strains was attended with a great deal of practical difficulty with the environmental conditions under which one has to operate at this station. The growing season is short. In order to grow properly a pullet for laying purposes it is necessary that she be hatched after April 1 and before June 1 *at the latest,* and preferably before May 15. If, however, one selects birds which produce no eggs whatever before March 1, and use up some valuable time before they get well started in the spring cycle of laying it becomes perfectly clear that one is automatically prevented from getting any considerable number of early hatched chicks from such mothers. If late hatched chicks are used the results obtained as to winter production later will not be critical. These circumstances make the propagation of a low producing strain on a large scale really a difficult proposition. There is of course no difficulty in breeding birds which will not be winter layers. One only needs to hatch in June, July or August. But such birds will furnish no critical evidence regarding the inheritance of winter production.

5. The mean winter production for whole flocks over the entire period of the investigation is 35.05 eggs. In

the writer's opinion, based upon rather extended experience in the study of egg records, approximately this figure may be taken as representing the general average winter production of mixed flocks of Barred Plymouth Rocks (or of American birds generally with the probable exception of White Wyandottes), which have been hatched at the proper time and well reared. As evidence on this point the data presented in Table II have pertinent bearing. These data give the mean winter production of birds of the different American breeds obtained in the Fourth Philadelphia North American International Egg-Laying Competition, carried on at the Delaware Agricultural Experiment Station in 1914–15. The conditions under which these records are made are such as to safeguard their essential accuracy. The figures here given are the mean productions per bird up to the end of the eighteenth and seventeenth week of the laying after November 1, 1914. Owing to the fact that the original records as published are compiled by calendar weeks it is not possible to give the exact production from November 1 to March 1. Eighteen weeks gives 5 days laying over this period, and seventeen weeks gives 2 days under. Both sets of means have therefore been tabled. It should be said that the birds were kept in flocks of 5 birds each, thus tending to the most favorable condition for high individual records.

TABLE II

MEAN WINTER PRODUCTION OF FOWLS OF THE AMERICAN BREEDS, CALCULATED FROM RECORDS OF THE FOURTH INTERNATIONAL LAYING COMPETITION, 1914–15

Breed	No. of Birds	Mean from Nov. 1 to Mar. 5	Mean from Nov. 1 to Feb. 26
Barred Plymouth Rocks	45	29.20	25.47
All Plymouth Rocks	80	32.39	28.39
All Wyandottes	55	48.20	44.00
All Reds	75	38.37	34.42
All American breeds	210	38.67	34.63

From this table it is clear that the records presented in Table I average about the same as those of the 210 birds of the American breeds in the Delaware competition.

The Wyandottes alone give a distinctly higher mean, and this the writer has also found to be true of Irish egg records. The Barred Rocks in the competition this year give a somewhat abnormally low winter mean. Irish records[6] give a winter mean for 48 Barred Rocks, in flocks of 6 each, of 36.54 eggs per bird which is more nearly normal.

III

Let us now turn to the question of the interpretation of the data set forth in the preceding section. Broadly speaking what the facts gleaned from this seventeen-year experiment show is that mass selection for egg production was *not* effective, while selection which was based upon the performance of the progeny *was* extremely and quickly effective. What is the explanation of the difference? The facts are purely objective realities, about which dispute or question is idle. They are real and obvious matters. Regarding the interpretation of such facts as these there have been, and no doubt will continue to be for some time to come, differences of opinion amongst biologists. Under these circumstances, the writer will, then, with all respect and consideration for the differing opinions of others endeavor to make clear the view of the meaning of these results which he has come to hold.

In the first place we may definitely put aside any interpretation which bases its explanation of the results on environmental action. In an earlier paper the writer[7] has shown in detail the impossibility of this explanation for the results during the period of mass selection (the descending limb of the curve). The totality of the results here presented make it still more apparent that such an explanation can have no place here. We should have to suppose that the environmental influences were adverse throughout the period of mass selection, but suddenly became favorable when the method of breeding was changed, and have ameliorated at an ever increasing rate

[6] Murphy, L., *Jour. Dept. Agr. Ireland*, Vol. XIV, pp. 8–30, 1913.

[7] Pearl, R., Me. Agr. Expt. Stat. Ann. Rept., 1911, pp. 113–176.

as time has gone on. Nothing of the sort was, in fact, the case. The only explanation which can satisfy the case is one which is based upon or at least takes full account of the changing genetic constitution of the flock.

It appears to the writer that the essential key-note to the explanation of the results of this long experiment is found in the fact that *phænotypic variation of the character fecundity, in fowls, markedly transcends, in extent and degree, genotypic variation.* It is quite impossible in the great majority of cases to determine with precision what is a hen's genetic constitution with respect to fecundity from an examination of her egg record *alone.* In this case, as in so many others, but in an unusually pronounced degree, where the phænotypic distributions overlap, a sure diagnosis of genetic constitution can only be made by means of the progeny test. Lacking this the phænotypic performance becomes an always uncertain and at times very misleading guide.

It can be shown that if, during the period of mass selection, all the hens used as breeders had been, as they were supposed in the theory of the originators of that part of the experiment to be, either Type 1 or Type 2 females ($fL_1L_2 \cdot \widehat{Fl}_2l_1$ or $fL_1L_2 \cdot \widehat{Fl}_2L_1$) then the continued mass selection must have resulted in improvement. The *only* criterion of constitution which was used, however, was the bird's performance. But, taken by this criterion alone, there would be constantly chosen a proportion of birds whose genotype was for mediocre fecundity, but which made a performance record (phænotypic) sufficiently high to be selected. That this is what actually happened is evident from the curve (Fig. 1), but the fact was experimentally proved in 1909.[8]

Put in the fewest words, then, the reason why no effect was produced during the first ten years of selection and a marked effect was produced during the last seven, was, in the writer's opinion, because genotypically high producers were *uniformly* selected (in the high lines) during

[8] Pearl and Surface, Me. Agr. Expt. Stat. Ann. Rept., 1909, pp. 49–84.

the latter period, and were *not* uniformly selected in the former. By the introduction of the progeny test as an essential part of the selection the whole process of the creation of a highly fecund race of hens was transferred from the realm of blind chance to that of precise and definite control. And it becomes increasingly clear that mass selection, on the basis of performance (phænotypic appearance) alone, is in its essential nature a blind and haphazard process, no matter with what precision and stringency it is carried out, just so long as the correlation between the gametic and somatic conditions of the character selected is not perfect. And it is an outstanding result of the Mendelian investigations of the last 15 years that the gamete-soma correlation is very rarely, if ever, perfect.[9]

It appears on this view that selection for high egg production in the fowl is effective when it is real. That is, if one selects *genetically* high producers by means of the trap-nest *plus* the progeny test, he succeeds very rapidly in fixing a high producing strain. If on the other hand he merely selects high layers by the trap-nest record alone, he is not really selecting genetically high producers except in a portion of the cases. Under these circumstances he makes no progress in building up a highly fecund strain. To be effective in changing the average productiveness of a flock of poultry selection must pick out those birds as breeders which carry the factors for high fecundity genetically, *i. e.*, as an integral part of their hereditary make-up, *and not any other birds.*

With the above interpretation of the results of seventeen years' continuous selection of the character fecundity, all the facts known to the writer are in complete accord. No other interpretation of the results of this experiment has yet been suggested which will meet all the facts.

[9] Complete citations on this point would make a tolerably full bibliography of Mendelism. The methodological or the strictly quantitative aspects of the problem have been but little dealt with. In this connection cf. W. F. R. Weldon, *Biometrika*, Vol. I, pp. 228–254, 1902, and R. Pearl, *Biol. Bulletin*, Vol. XXI, pp. 339–366, 1911.

IV

What bearing have these results upon the general problem of the effectiveness of selection in modifying germinal determiners? Let us at the outstart endeavor to be quite clear as to the problem. It has been shown in what has preceded that in the long experiment a change in the average condition of the population has occurred, and has been coincident with selection. The writer has no hesitation in saying that the increase in average productiveness since 1908 has been *caused* by the particular kind of selective breeding practised. Furthermore the average productiveness at the present time transcends any average known in the previous history of the stock.

Granting all this, however, as plain matter of fact, it does not, in the writer's opinion, afford one iota of evidence that through the process of selection the hereditary determiners of fecundity either have been or can be changed. All that the selection has done, so far as we have any evidence, is to change the constitution of the *population* in respect of fecundity genotypes. There is no evidence that the genotypes themselves have been changed. On the contrary, everything indicates that they have not been changed. During the last seventeen years we have merely sorted out from a mixed population, by a systematic method of breeding, those individuals which were alike in one respect, and have sold all the rest to the butcher. That one respect was that each individual bore progeny which were high producers.[10] Those individuals chosen as breeders in 1908 and 1914 were precisely alike in this particular There were more of them available in proportion to the whole flock in 1914 than in 1908, but, as individuals, I am unable to discern any particular in which they were different in 1914 from what they were in 1908.

The general point here involved is essentially the same as one with which we are more familiar in demographic

[10] I am, of course, referring to the high line selections only, merely for the sake of verbal economy. The same reasoning *mutatis mutandis* applies to the low lines.

statistics. The constitution of a population does not directly affect the individual. My expectation of life will not be materially increased if I chance to move into a community in which all the other inhabitants are of advanced age. To this everyone will agree. But the extreme selectionist appears to believe that in some mysterious way the act of continued selection, which means concretely only the transference of each selected individual from one cage or pen to another to breed, will in and of itself change the germ-plasm, so that after the act it is different from what it was before! It does not seem that the evidence that such is in fact the case is critically valid. A careful study of the very interesting and valuable work of Castle and Phillips[11] with rats leaves the writer with the feeling that those experiments prove no more than do the experiments here reported: namely that the composition of a population may be altered by selection. It does not appear to be proven that selection has essentially altered the constitution of the germ-plasm of any particular individual as compared with the germ-plasm of that individual's ancestors, making due allowance of course for the phenomenon of segregation. That selection can alter the composition of a population with respect to genetic determiners, by a process of sorting over what is already there and rejecting some portion, no one can doubt. But it still appears to the writer to be true that: "It has never yet been demonstrated, so far as I know, that the absolute somatic value of a particular hereditary factor or determinant (*i. e.*, its power to cause a quantitatively definite degree of somatic development of a character) can be changed by selection on a somatic basis, however long continued."[12]

[11] Castle, W. E., and Phillips, J. C., "Piebald Rats and Selection," Carnegie Institution of Washington Publication No. 195, 1914.

[12] R. Pearl, *Jour. Exp. Zool.*, Vol. 13, p. 264, 1912.

SPECIFIC AND VARIETAL CHARACTERS IN ANNUAL SUNFLOWERS

PROFESSOR T. D. A. COCKERELL

UNIVERSITY OF COLORADO

THE group of *Helianthus annuus*, the typical, annual sunflowers of North America, is not a large one. The annual habit seems to have been acquired independently by several different Helianthine stocks, so that *H. bolanderi* Gray, *H. exilis* Gray, *H. floridanus* Gray and *H. tephrodes* Gray are to be excluded from the *H. annuus* group. The subgenus *Helianthus* s. str., or *Euhelianthus*, contains the following:

1. *H. annuus* Linn. Based on the large cultivated form (*H. macrocarpus* D. C.), Dr. A. H. Church of Oxford has investigated the history of this plant, and I take the liberty of quoting from a letter he wrote on March 4, 1915:

> The published accounts of the giant sunflower in Europe in the sixteenth century are so precise that it is interesting to remark that this is in fact the *oldest* mutation known, which is *still* with us, quite unaffected, though still never quite a pure strain, owing to insect pollination. The facts are quite simple. The first description of the plant, by Dodonæus (1567), tells us it grew in the Botanic Garden at Madrid, *24 feet*. At the Padua Garden, *indoors*, in a viridarium or orangery, *40 feet!* The usual height was 20 ft. The first English specimens, grown in London by Gerard, were 14 ft.; and 15 ft. is the local record here. The giant form is known by carrying one *head*, and having no trace of axillary buds, = *Monocephalic* strain, as opposed to reverting branching individuals. . . . The next point is, where did it come from? *From Peru*, say the Herbals, but all Spanish things from America came *via* Peru, because this was the last port of call. Hence Mexico is regarded as the home. On the other hand *Ximenes*, who lived in Mexico several years, and *Hernandez* after him, call it the *Chimalacak del Peru*; "acak" I find means a *reed*, and thus refers to the long tall single stem of the cultivated crop. The inference is that the plant as we know it was evolved by ages of selection *in Peru*, by guano fed cultivation, possibly long before Inca rule, the plant having been taken by all migrating tribes from the Mexican district. . . . Regarded as a product of Peruvian agriculture the sunflower is curiously parallel with the *maize*. . . . It was the oil crop of ancient America.

The true *H. annuus* appears to be quite unknown in the wild state, but nevertheless the monocephalic character may have arisen among wild plants. Dr. Church makes the following suggestion:

> If the monocephalic form is the giant of cultivation derived from the Prairie form, it should be possible *to repeat* the history, by growing Prairie forms in quantity, and selecting the suitable mutations when they appear under the stimulus of excess manure (guano for choice). My idea has been that, knowing what to look for, it might be possible to get somewhere near it in say 10 years; though the Indians possibly took 2,000. General structural evidence alone suffices to show that the monocephalic strain is the response to selection for close cultivation (about two plants per square yard). The solitary heads are required for simultaneous harvesting.

2. *H. lenticularis* Douglas. The prairie sunflower, much branched, and normally with dark disc. It has been regarded as the wild type of *H. annuus,* but Rydberg treats it as a distinct species. In crosses with typical *annuus,* the F_1 is intermediate, often with a tendency to fasciation. If *annuus* and *lenticularis* are considered specifically distinct, we have to face the difficulty that the former is known only in cultivation, and its one "specific" character, the monocephalous habit, is not constant.[1] The color of the disc is not a reliable distinction, since yellow discs occur in wild plants. Possibly the variation shown by *H. annuus* may be explained by contamination with *lenticularis,* since some strains, at least, are constant in their characters. At present, however, it seems probable that no wild *species* ever existed with typical *H. annuus* characters; the actual facts would probably be best represented by considering *lenticularis* the species, and *annuus* a cultivated variety derived therefrom. Since, however, the latter was first named, the species-aggregate will have to be called *H. annuus,* and the nomenclatural outcome will be as follows:

[1] Shull, *Botanical Gazette,* **45**, 105, figures a much branched form which is not the wild *lenticularis.*

Helianthus annuus L.

(*a*) *lenticularis* (Dougl.)

(*b*) *macrocarpus* (D.C.) = *annuus* L., s. str.

At the same time, for ordinary purposes, it may be permissible to simply write *H. lenticularis* when referring to the wild plant.

3. *H. aridus* Rydberg. Like *H. lenticularis,* but leaves lanceolate or narrowly deltoid, minutely toothed or entire. Montana to New Mexico. Nelson calls this a synonym of *H. petiolaris,* which it certainly is not. It must be called *H. lenticularis aridus* (Rydb.) or *H. annuus lenticularis* var. *aridus,* since it is a variable form of *lenticularis,* which may possibly be due to crossing with *H. petiolaris,* the hybrid having crossed back with *lenticularis.* From the mode of its occurrence it is nearly certain that it is not a simple *lenticularis* × *petiolaris* hybrid, *petiolaris* being often absent from the immediate vicinity.

To give an idea of the actual condition of affairs where *H. aridus* occurs in Colorado, I present a synopsis of the forms found at Longmont, August 30, 1914:

(*A*) *H. aridus* type; smaller and more slender, with cuneate bases to leaves.

(*a*) Variety with yellow disc; two plants found.

Disc 19 mm. diameter, light yellow (corollas entirely dull light yellow); rays ordinary; foliage unusually pale; base of leaves rather broad-cuneate, marginal teeth feeble.

(*b*) Disc dark (corolla lobes dark reddish). Leaves with cuneate base and subentire margins; typical *aridus.* Involucral bracts *very* broad and bristly. These rather slender plants have small discs (17–21 mm. diam.) and very ample rays, which are not very numerous (10–13); color of rays rich orange yellow; stems lightly speckled with purplish.

(i) Rays longer, about 38 mm. long and 15 broad.

(ii) Rays shorter, about 28 mm. long and 14 broad.

(This difference in size of rays is probably environmental.)

(*B*) *H. lenticularis* type; bases of leaves truncate or cordate; plants usually more robust; disc dark.

(*a*) Aspect of *aridus,* being rather slender, with small (diam. 23.5 mm.) disc and long rays; but leaves broadly truncate at base and rather strongly toothed, *quite lenticularis* style. This is a very pretty form, with long rays (about 40 mm. long and 11 broad), more or less twisted at end, and rather narrow. The rays number about 15.

(*b*) Aspect of *lenticularis;* more or less robust, rays rather short and numerous.

(i) Rays comparatively short and broad (about 22 mm. long and 10 broad on a small head), the middle third beneath with its apical half variably light brownish-red. Leaves thick, with broad petioles.

(ii) Rays normal.

(α) Upper leaves ovate, scarcely at all dentate, inequilateral. Disc small (22 mm. diam.), rather paler than usual, the corolla lobes showing less red. Rays 14, about 31 mm. long and 11.5 broad.

(β) Upper leaves broad at base, but somewhat cuneate, rather feebly dentate. Disc 20–23 mm. diameter. A small head (disc 20 mm.) with many (21) quite *short* rays, about 17 mm. long and 7 broad.

(γ) Typical *lenticularis,* with broad-based strongly dentate leaves. Disc 37 mm. diameter; rays 37 mm. long, numerous (about 33).

It would of course be possible to maintain that *H. aridus* was originally a distinct or isolated species, which has now lost its purity by crossing with *lenticularis.* We can at least say this, that if *annuus, lenticularis* and *aridus,* in their pure forms, inhabited three different islands, few would hesitate to regard them as perfectly "good species." Also, if they grow mixed for any length of time, they are sure to suffer from "vicinism" to such an extent as to lose their supposed original distinctness. At present, however, we have no assurance that *H. aridus* has ever constituted a distinct species, in the sense of occupying any considerable area in its pure form. On the other hand, it is manifestly not a "fluctuating variation," due to mere environmental conditions.

4. *H. petiolaris* Nuttall. Described by Nuttall in 1821, from "the sandy shores of the Arkansa," and recommended as "an ornamental annual of easy culture." It extends from British America to the State of Chihuahua. It differs from *H. lenticularis* by (*a*) smaller stature, (*b*) leaves differently shaped, lanceolate or broad-lanceolate, not dentate, more or less shiny above, those of *lenticularis* being quite dull, (*c*) bracts of involucre lanceolate, with margin very short-ciliate. Stem rough, with a little purplish color; basal third of rays deeper orange than the rest.

This is a good species in the ordinary sense; in Colorado it is often found abundantly in the cañons of the foothills, growing without admixture of other species. Lower down, it frequently occurs with *lenticularis*.

The variety *patens* (Lehm.) Rydb. is said to differ by having the heads larger, long-peduncled, the peduncles fleshy toward the top; leaves large, long-petioled. Nuttall described his original *petiolaris* as having the peduncles "of great length," and the petioles "of an extraordinary length," though the leaves were "rather small." Probably *patens* is not far from the original *petiolaris*. Gray considered *patens* a synonym. According to Rydberg, the leaves of *patens* are broadly ovate or subcordate, much in the style of *lenticularis*, while the bracts are those of *petiolaris*, thus reversing the condition of *aridus*. It is possible that *aridus* and *patens* are both remote results of the *lenticularis* × *petiolaris* cross, but in the vicinity of Boulder, when *aridus* is common, I have not found *patens*.

5. *H. canus* (Britton) Wooton and Standley. A species of New Mexico, Chihuahua, and adjacent regions, close to *petiolaris*, but with abundant white pubescence on leaves and stems. The involucral bracts are of the *petiolaris* type. This is to *petiolaris* much as *H. argophyllus* is to *lenticularis*, but the pubescence is long and spreading, not subappressed and silky.

6. *H. argophyllus* Torrey and Gray. Discovered by Drummond in dry soil in Texas. This has the form and leaves of *lenticularis*, but is very remarkable for the long subappressed silky white hairs, totally different from those of any other *Helianthus* known to me. Gray remarks that it "degenerates in cultivation apparently into *H. annuus*," which merely means that it suffers from vicinism. Old cultivated stocks, kept pure, are quite constant. A remarkable feature of *H. argophyllus* is the extremely slow growth, at least until near flowering time. This peculiarity is dominant in a cross with *H. annuus* × *lenticularis*.

7. *H. debilis* Nuttall. Florida to Texas.

8. *H. praecox* Engelm. and Gray. Florida to Texas, near coast. Differs from *debilis* by being strongly hirsute.

9. *H. cucumerifolius* Torrey and Gray. Texas. Differs from *debilis* and *præcox* by having the branches mottled with purple.

The last three were eventually reduced by Gray to a single species, but Small keeps them separate. My wife and I have grown *H. cucumerifolius* for several years, and have crossed it with *annuus* × *lenticularis*. The first cross is quite fertile, but it is impossible to get any quantity of F_2 seed. Mr. Leonard Sutton in England has had the same experience; he writes (April 3, 1915)

> We are arranging for a large breadth of the *cucumerifolius* crosses this season, but we have found as you mention that very little seed is produced, and we are hoping that the plant will improve in this respect if grown for a few years, and the best seeding plants are selected for stock.

These hybrids are of considerable horticultural value, especially those derived from crosses with the red sunflower, so it is desirable to secure fertile strains if possible. Something may be attained by crossing back with the parent species.

The *H. cucumerifolius* type is dwarf, freely branching, with broad bright green leaves, shiny on both sides. The involucral bracts are long and narrow. The bulb or swelling of the disc corollas is minutely puberulent, whereas that of the *lenticularis* forms is long hairy. In the F_1 hybrid the bulb is long-hairy as in *lenticularis*, the character being dominant. Although *H. cucumerifolius* is very unlike the other species (except *debilis* and *præcox*) in apperance, its constant structural differences are very few. The base of the leaves, as in the *annuus* forms, may be auriculate or truncate. The disc bracts may be long-ciliate, or with the margins merely appearing scurfy. It is proper to state that my material belonged to cultivated strains; possibly the wild plant is less variable.

Thus we have at the most nine species, which can probably be reduced to five. They belong to the region which used to be marked in old geography books as the "Great American Desert," though members of the *debilis* group extend along the Gulf States to Florida. The dominant, widely distributed form is *lenticularis*, a plant of sandy river-bottoms and similar places, which has spread as a weed in cultivated areas. Prior to the era of cultivation it is probable that *H. petiolaris* occupied a greater area, at least in acreage. At the present time *H. lenticularis* is common in California, but I suspect that it has been introduced into the Pacific coast region by man.

In order to give an idea of the cultivated forms of our group, I have made a table from Sutton's Catalogue for 1915.

Silver-leaved (*argophyllus*-type); rays yellow; disc black; 5 ft. ..... *Silver-leaved.*
Not silver-leaved ..... 1.
1. *Cucumerifolius*-type, none over 4 ft. high ..... 2.
Annuus-type, mostly tall ..... 6.
2. Only 12 inches high, compact ..... *Dwarf Miniature.*
Four feet high ..... 3.
3. Rays rolled, like the cactus dahlia ..... *Orion.*
Rays not rolled ..... 4.
4. Rays pale primrose, disc dark ..... *Primrose Stella.*
Rays bright yellow ..... 5.
5. Heads small, with dark disc ..... *Miniature.*
Heads larger, rays long ..... *Stella.*
6. Rays wholly or partly chestnut red ..... *Red.*
Rays wholly or partly vinous ..... *Langley Gem*
Rays primrose ..... 7.
Rays bright yellow or orange ..... 9.
7. Double (i. e., disc florets ligulate) ..... *Double Primrose.*
Single; disc black ..... 8.
8. Tall, 6 ft. high ..... *Primrose Perfection.*
Dwarf, 2.5–3 ft. ..... *Single Dwarf Primrose.*
9. Double (*i. e.*, disc florets ligulate) ..... 10.
Single (*i. e.*, normal heads) ..... 11.
10. Flowers orange; 6 ft. ..... *Double* (also a double 5 ft. high).
Compact habit; 3 ft. ..... *Dwarf Double.*
11. Heads extremely large; height 8–10 ft. ..... *Giant.*
Heads ordinary or smallish; disc dark; height 6 ft. ..... 12.
12. Heads medium size ..... *Æsthetic Gem* (J. Veitch & Sons).
Early flowering ..... *Earliest of All.*

Of the above *Red* is *coronatus*, and *Langley Gem* is *vinosus*, both derived from our Boulder cultures. The seed offered as Langley Gem was grown in Boulder. The *Primrose* variety I have called *primulinus*.

An old cultivated variety is *H. annuus* var. *indicus* (*Helianthus indicus* Linn., Mant. I, 117), peculiar for the foliar expansion of the involucral bracts. It did not come from India, but from Egypt. *Tithonia speciosa*, once regarded by Hooker as a *Helianthus*, has the bracts normally foliaceous. In 1913 I witnessed the appearance of foliaceous bracts in the F_2 generation from *primulinus* $\times$ *coronatus*. The plant in question was a very abnormal dwarf, wholly unlike the rest of its generation, or any known parents. It was described as follows:

Dwarf, about 28 mm. high; slender, fasciated at top of stem; rays vinous, but on nearly all the heads a very dilute and dingy color; disc dark, stigmatic branches dark red; apical part of disc corollas dark greenish, tipped with red, and very hairy; anthers not projecting, but not shrivelled, almost wholly without pollen, and what there is probably no good; achenes hairy, usually with supernumerary pappus scales; pappus scales stained with pink; involucral bracts long and tapering, strongly hirsute, curled over, one or two outer ones long and foliaceous; stem hirsute; leaves long and narrow, narrowly cuneate at base; margins irregularly, sharply dentate, entire on small very narrow leaves; sometimes one of the large lateral veins of the leaves, and its supporting tissue, absent.

Such a plant may result from some unwonted combination of genes, whereby the normal constitution is broken down and in the resulting disruption characters usually suppressed appear. Such monstrosities quickly perish, but during their transient existence may reveal, like a drunken man, matters which in the well behaved would never reach the surface.

One of the most remarkable of cultivated varieties is the *Chrysanthemum-flowered*, of which we obtained a

perfectly constant and uniform strain from Dreer. It may be named var. *chrysanthemoides;* plants of the same general type have passed in horticulture as var. *californicus* (not *H. californicus* D.C.)

Helianthus annuus var. *chrysanthemoides*

Manner of growth.—(Tested in two seasons). Grows much more slowly than the other forms (except *argophyllus),* but is very robust. Nine plants studied were 15–17 inches high July 14, about 36 inches July 30, and coming into flower at about 5 ft., 6 inches, August 15.

Foliage.—At first (June 8) leaves are narrow and long; very uniform. Later, the upper (small) leaves are conspicuously pallid. At time of flowering the leaves are broad, cordate, with auriculate base; surface very strongly crinkled; margin moderately dentate.

Pubescence.—Leaves soft with very scanty pubescence; petioles somewhat scabrous; stems, especially toward the top and under the heads, with abundant and conspicuous soft white pubescence.

Heads.—Stalks greatly broadened under heads, diameter about 27 mm. just under bracts; involucral bracts hairy, the marginal hairs not longer than those covering the backs of the bracts, five strong veins, and others weak; basal half of bracts about 15 mm. broad, gradually, not abruptly, tapering to acuminate ends; bracts extending about 18 mm. beyond outer florets, which are like the inner ones; heads entirely double (*i. e.,* corollas ligulate), rays very bright orange or saffron, discs light green before they come into flower; immature achenes with much silvery hair.

This plant is so distinct, structurally and physiologically, that if it were not known to have originated in cultivation, it might well pass as a distinct species. Although I have no information concerning its history, I can only suppose that it is part *argophyllus.* Mr. Leonard Sutton writes me that the similar *Double* catalogued by him, which is of continental origin, does not grow more slowly

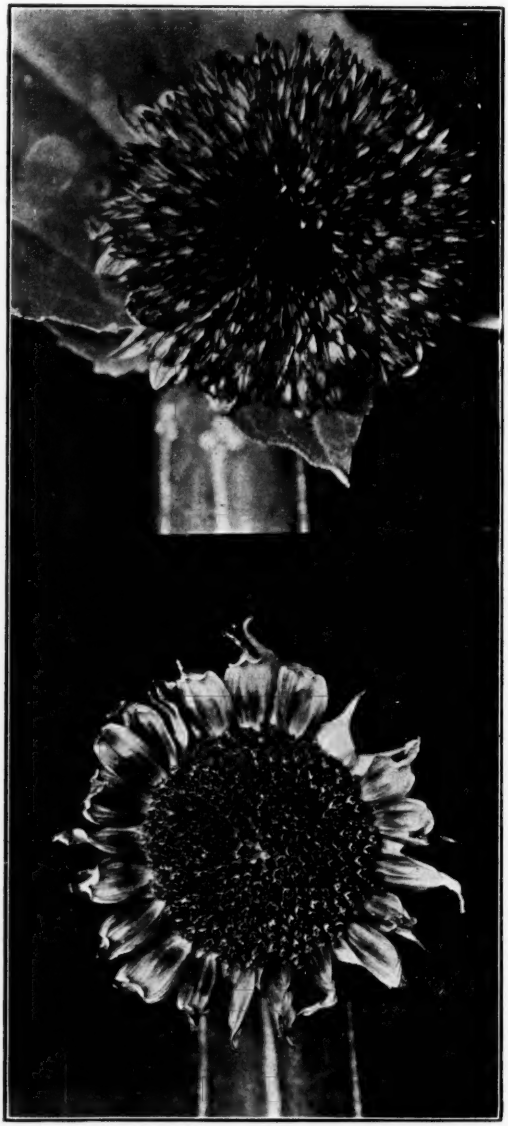


FIG. 1, above, Double Red Sunflower. Fig. 2, below, Helianthus von tortuosus.

than other sunflowers in its early stages. The var. *chrysanthemoides* was found by us to cross freely with the *annuus* × *lenticularis* varieties, producing a series of semi-doubles. The double and semi-double forms extracted from this cross and from crosses with Sutton's various double forms need not be described here, but in order to illustrate the double type, I give a figure of a full double with chestnut color, the red being derived from the variety *coronatus* (Fig. 1).

Modifications of the Rays

Number.—Halsted (Rept. Bot. Dept. N. J. Agric. Exp. Sta. for 1911, pp. 335–337) has given elaborate data from the branched form of the cultivated *H. annuus*, showing that the terminal heads have most rays, and when there are many lateral branches, the rays on these are comparatively few. Nevertheless, there are inherited differences in the number of rays, not depending on conditions of nutrition. I observed a striking case by the roadside in Boulder, where three wild *lenticularis* plants, growing close together, differed thus:

(*a*) Rays normal, at right angles to axis; number of rays in well-formed heads, 21, 21, 21, 21, 20, 21, 21.

(*b*) Rays normal, elevated, their plane oblique in relation to the axis of head; rays in well-formed heads, 14, 13, 14, 14, 14, 11, 15.

(*c*) Rays set obliquely, but less so than in *b*; rays in well-formed heads, 18, 18, 18, 19. In this plant many of the rays were modified by quilling and splitting, some being completely quilled, *i. e.*, hollow and tubular. The normal rays were very obtuse, and distinctly emarginate at end. Some showed a little red color on apical part of middle third beneath.

Length.—The length also differs, the differences due sometimes to race, sometimes to illumination or nutrition. In our cultures mutational forms have arisen with unusually short rays, thus:

(*a*) Var. *vinosus* with disc 55 mm. broad, rays only 35 mm. long; disc unusually convex.

(*b*) Var. *bicolor* with disc 64 mm. diameter, rays only 29 mm. (Next to it, in the same lot, grew a plant with disc diameter 38, rays 47 mm.)

These measurements represent average heads from the respective plants. A quite analogous variation was seen in two plants of *Ratibida columnifera,* growing at Boulder along with the typical form (var. nov. *breviradiata,* rays yellow, only about 10 mm. long, about half the normal size).

Torsion.—A peculiar form which appeared in our cultures is the variety *tortuosus,* in which the ends of the rays are twisted, as though in curl papers. This is wholly unattractive, but other variations have the long rays moderately curled or twisted, promising the development of a series of forms analogous to the cactus dahlias. As with the cactus dahlias, the rays may be rolled instead of twisted; a wild form of this type may be described thus:

Helianthus lenticularis var. n. *angustus.* Rays about 20, narrow, rolled, so that they are separated by wide intervals. The rays were 36 mm. long and 5 wide (a normal *lenticularis* ray 30 mm. long is 9 wide). Disc 26 mm. diameter. Goodview, Colorado, July 28, 1913.

Tubular Rays.—Under the heading "Number" above, a case of completely quilled rays in a wild sunflower is recorded. This peculiar modification indicates some deep-seated tendency in the Compositæ, since it appears in several genera, *e. g.:*

(*a*) *Ratibida columnifera* var. n. *tubularis.* Rays of the usual orange color, about 25 mm. long and 3.5 broad, completely quilled, being hollow cylinders. Flagstaff Hill, Boulder, Colorado, July 19, 1914.

(*b*) *Rudbeckia hirta* var. *tubuliforme* S. H. Burnham Amer. Botanist, Feb., 1914.

(*c*) *Gaillardia pulchella* var. *fistulosa* (*G. fistulosa* Hort.).

Emarginate and Cleft Rays.—This is another common modification, also observed in other genera, as *Ratibida* (*R. columnifera* var. n. *incisa;* rays with one or two deep

incisions, and also some narrow supplementary rays; Boulder, Colorado, August 8, W. P. Cockerell).

Double Rows.—The disc remaining normal, the rays may be in two rows, indicating an approach to a type resembling the star dahlias.

Color.—The yellow may be of various shades from deep orange to very pale, approaching white. This has already been discussed in *Science,* August 21, 1914, pp. 283–285. It may be possible eventually to get a pure white. Dr. Church (in litt.) refers to a white form as having been mentioned long ago by Hernandez. There is also the development of the soluble (anthocyanin) red pigment, giving us the chestnut red and wine red varieties.

Conclusions

It is impossible at the present time to give all the evidence on which opinions have been formed, but such facts as are reported above, and others, seem to suggest the following generalizations:

1. The number of genes or determiners in *Helianthus* is not infinitely great; it is probably very much less than exists in most animals, and the study of the processes of heredity is relatively simple.

2. In the history of the sunflowers of the *H. annuus* group, there have been few really new developments. Species which seem very distinct prove on examination to have few special characters of their own.

3. It is quite common for variations to arise, in wild and cultivated plants, which appear to break the type, and initiate something altogether new. When, however, we begin to gather data on the variation of the Compositæ, we find that practically all these "new" variations repeat themseles in various species, and at various times, indicating that they represent deep-seated common tendencies. Their occurrence among wild plants shows that they are not necessarily connected in any way with cultivation, and it is equally evident that they need not indi-

cate any sort of hybridization. For example, *Ratibida columnifera* presents many variations parallel with those of *Helianthus,* in localities where it is the only species of its genus.

4. We are led, then, to think of the annual sunflowers as plants representing a certain complex of potentialities or genes (of which we may hope at length to make a reasonably complete catalogue), offering these in different combinations at different times, usually failing to register any permanent advance, but once in a long while reaching a new position of stability, suited to a particular environment. These positions of stability represent what we call the species. As with the dahlia, the horticulturist may expect to be able to produce many interesting varieties by selecting and saving the various possible combinations, but analysis shows that the genes going into these are the old ones, the effects of which may be seen from time to time even in wild plants.

The perennial sunflowers appear to offer a more complex problem. Mr. S. Alexander has found hundreds of what are considered "elementary species" in Michigan. He has been good enough to send me a large number of these, and I can testify that they are appreciably different; yet they seem to represent recombinations of old characters, already known to exist in the species of the manuals. Some would dismiss them, along with the multitudes of *Cratægus,* as hybrids; but it does not seem justifiable to assume hybridization without better evidence. We have sufficient proof, I think, that all sorts of new combinations of characters may arise within a type, without hybridization.

Undoubtedly new determiners are formed (how, we need not here speculate) from time to time, but the occurrence must be so rare and so difficult to demonstrate that we can hardly hope to obtain satisfactory evidence concerning it.

THE INHERITANCE OF DOUBLENESS IN MATTHIOLA AND PETUNIA. I. THE HYPOTHESES*

HOWARD B. FROST

CITRUS EXPERIMENT STATION, UNIVERSITY OF CALIFORNIA

THE peculiar inheritance of "doubleness" in stocks (*Matthiola*) has long been a matter of special interest. Some races produce only single-flowering plants. A pure double-flowering race, on the other hand, is an impossibility; the doubles are absolutely sterile, stamens and pistils

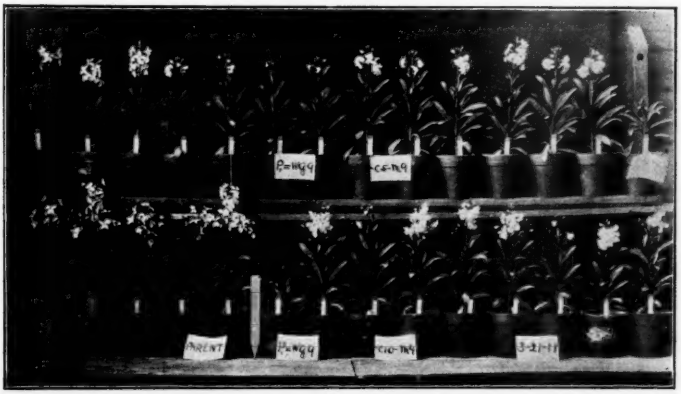


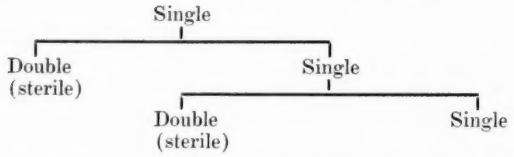
FIG. 1. *Matthiola* plants, unselected progeny of two parents, showing the mixture of singles and doubles invariably given by this variety ("Snowflake"). Note that the singles, in these cool-greenhouse cultures, differ little from the doubles in earliness of flowering. (The singles and doubles have been separated for photographing. The singles are plants 1, 2, 3, and 11 (misplaced), from the left side, in the upper row, and plants 1 to 5 in the lower row.)

being entirely absent. Certain races, however, consist of both singles and doubles, in nearly equal numbers,[1] each generation being descended from the singles of the pre-

* Paper No. 17, Citrus Experiment Station, College of Agriculture, University of California, Riverside, California.

[1] The usual proportion of doubles in large cultures seems to be near 53 per cent., or perhaps slightly higher in some cases.

ceding generation (see Fig. 1); the following diagram shows the mode of inheritance in such races:



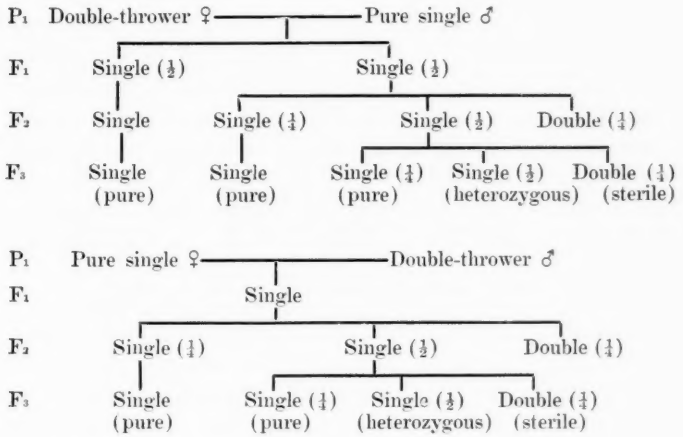
Miss Saunders (1911; 1913; Bateson, 1909, pp. 201–204) has done a great amount of work on heredity in *Matthiola*, and has developed an ingenious hypothesis to explain the peculiar behavior of doubleness. Goldschmidt (1913) has given another explanation, which has been vigorously criticized by Miss Saunders. Several years ago (perhaps in 1909), largely on the basis of Miss Saunders's evidence, I formulated a hypothesis somewhat simpler than either of those just mentioned.

In view of the special interest of the case at present, and the fact that one or both of the essential points of my explanation have been suggested incidentally by another writer (Belling, 1915, 1915a), it seems desirable to give a general review of the hypotheses at this time.[2]

As Miss Saunders's (1911; Bateson, 1909, p. 201–204) crosses have shown, the "double-throwing" singles are heterozygous, the approximately 1:1 ratio being due to the fact that the functional pollen is all double-carrying. This is shown by Miss Saunders's crosses between double-throwers and pure singles. When the double-thrower is the seed-parent, about half the F_1 progeny are heterozygous, the rest being pure singles; about half the double-thrower eggs, then, are "double-carrying." On the other

[2] My own data bearing on the problem have largely been published (Frost, 1911) or will be published in two papers (Frost, unpublished) soon to appear; some further evidence, relating to the proportions secured with some 8,000 plants of one variety, together with a summary of my other data, is to be presented in a paper to follow the present one. Aside, however, from one important general feature of these results, to be briefly stated below, the view given here is dependent on Miss Saunders's evidence and that cited by her.

hand, when the double-thrower is the pollen-parent, *all* the F_1 progeny are heterozygous; hence all the double-thrower-pollen is double-carrying. These facts are illustrated by the two following diagrams (adapted from Goldschmidt):


P1 Double-thrower ♀ Pure single ♂
F1 Single (½) Single (½)
F2 Single Single (¼) Single (½) Double (¼)
F3 Single (pure) Single (pure) Single (¼) (pure) Single (½) (heterozygous) Double (¼) (sterile)
P1 Pure single ♀ Double-thrower ♂
F1 Single
F2 Single (¼) Single (½) Double (¼)
F3 Single (pure) Single (¼) (pure) Single (½) (heterozygous) Double (¼) (sterile)

In these two crosses, *where the "singleness" in the F_1 (or later) heterozygotes comes entirely from the pure single parent*, we get what seems to be an ordinary Mendelian[3] result in F_2; the pollen of these heterozygotes must carry both "singleness" and "doubleness." The absence of singleness from the double-thrower pollen is taken by Bateson (1914, p. 292, foot-note) as almost conclusive evidence of somatic segregation of factors, occurring in such a way that the pollen-mother-cells receive only doubleness. Neither he nor Miss Saunders, however, gives any reason why singleness, rather than doubleness, should be thus eliminated. Goldschmidt (1913) and Belling (1915, p. 126) have stated that selective sterility of pollen will also explain the case, and definite evidence for this view is presented below.

[3] In some crosses the proportion of doubles is smaller, possibly 1/16 instead of 1/4.

To explain the slight but constant excess of doubles over singles, Miss Saunders assumes that two complementary linked factors, X and Y, are essential to singleness, and that these factors cannot be carried by the male gametes of the double-throwers, which are all xy. X and Y are supposed to be so linked in the ovules that the four kinds of eggs are produced, not in equal numbers, but in the ratio 7XY : 1Xy : 1xY : 7xy—or else in the ratio 15 : 1 : 1 : 15. Fertilization by xy pollen will give, in the former case, $7XY \cdot xy + 1Xy \cdot xy + 1xY \cdot xy + 7xy \cdot xy$; if only zygotes having both X and Y are single-flowering, only the first class will consist of singles, and the doubles will constitute 9/16, or 56¼ per cent., of the total. Linkage on the 15 : 1 plan would give 17/32, or 53⅛ per cent., of doubles.[4]

For certain cases where crosses with pure singles have given much less than 25 per cent. of doubles in F_2, Miss Saunders assumes the presence of a second set of two linked factors, X′ and Y′; then any zygote receiving X or X′ together with Y or Y′ is a single, and the proportion of doubles is correspondingly reduced.

Von Tschermak (1912) favors Miss Saunders's hypothesis; he suggests the possibility of selective elimination (in a dihybrid scheme), but does not consider this explanation probable. It would seem, however, in view of considerations stated below, that any dihybrid scheme to explain the usual slight deviation of the double-throwing races from a 1 : 1 ratio is unnecessarily complex.

Goldschmidt's (1913) hypothesis assumes selective degeneration or sterility of pollen in the double-throwers, and considers the case to be one of sex-linkage, classing the slightly aberrant ratio with the known cases of slight deviation in the sex-ratio in animals. He supposes that this "hermaphroditic" plant is homozygous for a distinct factor for femaleness (F), producing eggs all of which carry this factor. He assumes that singleness is

[4] Miss Saunders (1911) rather favors the latter gametic ratio, which also corresponds closely to my own data.

determined by one dominant factor, S; the eggs of the double-thrower, then, are SF ("single") and sF ("double"). He assumes, also, that half the pollen-grains or microspores, in all races of *Matthiola*, lack F, probably because of elimination of part of an X-chromosome, and *that these pollen-grains degenerate* or at least are non-functional, so that no staminate plants are produced. It is necessary to assume, then, that in the double-throwing races S (or s) and F are carried by the same chromosome, and that the S-carrying chromosome is always the one to eliminate F. The S-carrying chromosomes will then be the ones destined to degenerate. The pollen resulting is of two kinds, Sf ("single," non-functional), and sF ("double," functional).

The double-throwing plant, then, is SFsF; its eggs are SF and sF, while its pollen-grains are Sf (non-functional) and sF. Self-pollination gives, then, SFsF (heterozygous or double-throwing singles) and sFsF (homozygous sterile doubles).

The factor S, however, can not in itself, in general, insure pollen-degeneration, since homozygous singles (SS) produce fertile pollen. Nor can the case be one of degeneration of all pollen-grains receiving *a maternal X-chromosome*, as is proved by the results of crossing SS and Ss races. Heterozygous singles (Ss) which get the S factor from a pure single (SS) parent, either through egg or through sperm, produce good S pollen, as is shown by the ordinary Mendelian ratio among their progeny (1 homozygous single (SS) : 2 heterozygous singles (Ss) : 1 homozygous double (ss). Goldschmidt is driven to assume, therefore, that the singleness factor (S_1) in the double-throwers differs from that in the pure singles (S)—or else to suppose that another factor interferes in the former type.

It will be seen that Goldschmidt gives, at most, only an indefinite implied explanation of the deviation of the double-single ratio from equality in the double-throwing races. And it is hard to see what advantage is secured

by introducing sex-factors into the discussion at all, when all actual individuals have both stamens and pistils, or else neither. When we assume—as Goldschmidt does—that the factor S is so modified in the double-throwing races as to insure the sterility of pollen-grains receiving it, the known facts must follow; it seems wholly superfluous to refer the sterility to linkage of S_1 with a sex-factor. The hypothesis seems quite unnecessarily complex; there is no real evidence here for the existence of a distinctly heritable femaleness factor, or for any elimination of sex-factors in pollen-formation, or for the occurrence of non-functional pollen in ordinary pure single (SS) races.

In a reply to Goldschmidt, Miss Saunders (1913) gives a very clear presentation of both her formulation and that of Professor Goldschmidt, urging most of the objections to the latter scheme which are stated above, but especially emphasizing its failure to explain the excess of doubles over 50 per cent. She also objects to the assumption of the existence of non-functional pollen, but I can not agree with her on this point.

I have sectioned anthers prepared for cytological study, and have frequently observed stages subsequent to the reduction divisions. The spore-tetrads appear normal, and there seems to be no early and conspicuous evidence of later degeneration. The "single" pollen, however, might even germinate and yet be strictly non-functional because of weak growth; and, as is shown below, the singles are actually inferior to the doubles in vigor. Selective partial sterility seems to be a rather common phenomenon, and it very probably occurs here.

The only other recourse seems to be the hypothesis of somatic segregation mentioned above, and somatic segregation, except as a rare accident of abnormal cell-division, has no decisive evidence in its favor[5] and an overwhelming convergence of probabilities against it. Belling (1915) calls attention to decisive evidence against

[5] Bateson's (1914, p. 292) positiveness in its favor seems to depend on just such cases as that here in question.

it in five genera representing as many distinct orders. Bateson himself (1909, chap. 9) reports a fact which seems to exclude it in the sweet pea, *although his reduplication hypothesis*[6] (Bateson and Punnett, 1911) *would require it there if anywhere.*

This phenomenon is one to which East (1915, p. 87) has recently referred, the "zygotic" nature of certain pollen-grain characters. In the sweet pea, for instance, F_1 hybrids between certain races with long (dominant) and round pollen have the pollen *all long,* although segregation, on any hypothesis, must have already occurred before the shaping of the pollen-grains. If segregation takes place as a result of chromosome-reduction, in the formation of the spore-tetrads, it is not strange that the cytoplasm of the young pollen-grain still retains the impress of the diploid maternal set of chromosomes, so that the pollen-grains give no evidence in their shape of the segregation that has just taken place. On the other hand, if segregation takes place early enough to permit of extensive "reduplications" of the cells carrying certain combinations of factors, it is very strange that the cytoplasm of the pollen-grain should be essentially maternal in nature. Especially does this evidence negative any hypothesis of cytoplasmic segregation—and if segregation is nuclear, surely we have reasons enough for connecting it with the reduction of the chromosomes.

It is due to Goldschmidt's hypothesis to note that a factor "completely coupled" with S, completely lethal for pollen and only slightly so for the embryo-sac, would explain the peculiarities of the case in *Matthiola,* both the non-functioning of the S-carrying pollen and the excess of doubles over 50 per cent. This is an amplification of his suggestion, in a passing reference (1913, p. 81), of a

[6] Bateson and Punnett explain linkage of genetic factors by means of the hypothesis of somatic segregation. They assume that a period of cell-division intervenes between the segregation of Mendelian factors and the formation of the germ-cells, and that the cells bearing certain sets of factors divide more often than the rest. This would result in making some classes of germ-cells more numerous than others.

possible "further distinct hereditary factor"; I merely omit the sex-factor, and suppose the other factor to be lethal in itself. He evidently does not notice that this sort of factor might well explain more than the sterility of the pollen. It amounts to the same thing, however, to suppose the double-thrower S (or S_1) to be itself the lethal factor. The introduction of sex-factors seems entirely unnecessary here, and the supposed lethal elimination of an F factor can not be general in hermaphroditic plants, since it would involve the universal occurrence of sterile microspores or pollen.

Our case appears to be merely one of a hybrid showing selective sterility of pollen-grains, a sterility due to the S factor or to a lethal factor linked with S. Further, if there is also a slight tendency to selective elimination of S-carrying eggs, we have a simple and direct explanation of the excess of doubles over the expected 50 per cent. Or, if the s-carrying eggs are more often fertilized, the excess of doubles is explained. Once more, selective elimination of single (Ss) embryos might produce the same result.

There are several facts which are extremely suggestive in relation to all these possible forms of selective elimination. First, it is known that, in a double-throwing race, the doubles are longer-lived than the singles in the seed stage; Miss Saunders (1911, p. 362) has definitely confirmed the common belief that the proportion of doubles tends to increase with the age of the seed. Second, Miss Saunders (1911, p. 364) has obtained a higher proportion of doubles from seed of lower viability, even with fresh seed. Third, some seed-growers (deVries, 1906, p. 335) regularly "starve" the seed-bearing plants, in the belief that they thus increase the percentage of doubles among the progeny. Fourth, the writer (Frost, 1911) has found, with one variety, that inhibition of flowering by high temperature is much more marked with singles than with doubles; in field cultures, in many cases, hot weather greatly delayed or entirely prevented flowering, the

difference there being very much greater than that shown in the tables in the paper cited.[7] Fifth, in the cultures just mentioned the doubles had larger leaves than the singles and evidently were decidedly larger as young plants. It seems that the double form (ss) is superior to the heterozygous single (Ss) of this double-throwing race in general vegetative vigor, and a similar difference may exist between s and S gametes; *on these facts probably depend the peculiarities of the observed ratio.*

In order to make the case of doubleness in *Matthiola* as clear as possible, let us consider a brief summary of the formulations that have been proposed. There are two essential points to be explained, namely: (1) the fact that the singleness factor or set of factors of the double-throwing races can not be carried by functional pollen, although the corresponding factor or factor-group of the pure single races so far tested is normal in relation to pollen, even in single-double hybrids; (2) the fact that the double-throwing races show a small but fairly constant excess of doubles over 50 per cent.

Miss Saunders gives a formally adequate but rather complex factorial hypothesis for (2). She leaves (1), however, essentially unexplained; she evidently relegates it to the realm of somatic segregation, and in any case makes no suggestion as to the real cause of the *uniform* elimination of *singleness.*

Goldschmidt, on the other hand, gives for (1) a hypothesis of selective sterility which is adequate, though of obviously unnecessary complexity, but fails with (2) about as completely as Miss Saunders does with (1).

It is here maintained that an extension of the general idea of selective elimination or viability, in any one of the several forms consistent with the evidence, complies with all the requirements, adequately explaining both (1) and (2). It might seem, at first thought, that the assumption of a difference between S and S_1, or of the exist-

[7] This evidence is to be published mainly in my forthcoming paper on "Mutation in *Matthiola.*"

ence of a distinct linked lethal factor, makes this scheme as complex as that of Miss Saunders; this is not the case, however, since Miss Saunders's scheme simply omits any attempt at real explanation of the peculiarity of the double-thrower pollen; her formulation imperatively requires the addition of the hypothesis of selective viability, or of some definite equivalent for it.[8]

The real puzzle of the case lies in the fact that the double-throwers plainly differ from the pure singles so far tested in at least two respects—heterozygosity for singleness (ability to form sporophylls) and the association of some peculiarity with the remaining singleness. This, however, is essentially a problem of the *origin* of the double-throwing races, and is, in any case, nowhere simpler than with the hypothesis here suggested. Miss Saunders's scheme really implies four factorial or linkage differences between pure singles and double-throwing singles, and for certain cases six such differences, in place of the two or three required by the hypothesis here favored. That is, the double-thrower is supposed to differ from the pure single in the following points: (1) that it is heterozygous for two complementary factors (X and Y) for which the pure single is pure, and in some cases also for a second set of such factors (X′ and Y′); (2) that its "singleness" can not be carried by functional pollen; (3) that X and Y are partially instead of completely linked. It is here proposed to drop half the factors of (1), and this makes (3) superfluous.

[8] She supposes (Saunders, 1911, p. 334) that X and Y are completely linked in the pure singles, but only partially so in the double-throwers; this explains why, with self-pollination, the latter give 50 + per cent. of doubles rather than 50 per cent., *but not why they approximate 50 per cent. instead of 25 per cent.* It would seem, however, that the Ss hybrid between pure single (SS) and double-thrower (S_1s) may usually give double progeny approximating, not the 25 per cent. assumed, but a *slightly lower ratio.* A possible general slight deficiency of doubles in this cross is not provided for in Miss Saunders's hypothesis, complete linkage of X and Y explaining why there is not an *excess* of doubles; whether the viability-hypothesis is adequate depends on the general viability-relations of the S factor (as distinguished from S_1), which quite possibly is even superior to s in respect to vigor.

It must be admitted, however, that (3) is not in itself improbable if (1) is true, in view of Miss Saunders's evidence. A similar difference between races, with respect to linkage, occurs with "cream" flower-color, which is partially linked with doubleness in the sulfur-white races, but completely linked in the pure-cream races. The essential difference of the viability-hypothesis, as here presented, relates to (1); the demonstrated lower viability of the singles, evidently the basis of (2), makes possible the simplification of (1).

If we accept this viability-hypothesis, there seem to be two general possibilities as to the origin of the double-throwing races. One is that the mutation by which Ss (double-throwing) races arise from SS (pure single) races involves a simultaneous or consequent alteration in the remaining S factor (or the production of a lethal factor completely linked with S), by which the presence of S becomes incompatible with pollen-formation. Second, it may be that the particular race or races in which our double-throwing forms originated had an S factor originally different from that of the pure single races which have been used in crossing with double-throwers—that is to say, an S factor originally incompatible with the formation of good pollen in an Ss plant—or else that they originally possessed the lethal factor suggested. If the second supposition is correct, such pure single races may be found,—races which in crossing with double-throwers *never give the F_2 ratio 3 singles:1 double, but only approximately 1 single:1 double.*

With *Petunia,* if we ignore the new seed-producing double (Francis, 1913), which has a distinct type of flower, the general case would seem to be similarly simple. Here, as is well known, the doubles are produced only when singles are pollinated by doubles, the ordinary doubles having stamens but not pistils, or, at most, non-functional rudiments of pistils. In this case the doubleness factor (D) is plainly dominant, and is perhaps to be considered an inhibitor; the single, then, is

dd, and the double Dd, cross-pollination giving 1dd:1Dd. There is usually (Saunders, 1910) an excess of *singles;* here, as in *Matthiola,* the heterozygous form is the one deficient in numbers, and it is also the one which appears inferior in vegetative vigor.[9] Probably the deviation from the 1:1 ratio is due in *Petunia* to selective elimination of *doubleness.*

We have, then, in *Matthiola* and *Petunia,* hybrids evidently due, not to the crossing of widely different forms, but to mutation within the race,[10] and yet they are partially sterile, and perhaps even lacking in vegetative vigor because of their hybridity! In connection with the vigorous discussion of mutation now going on, it seems worth while to ask whether, in a case like that of *Œnothera,* hybridization is the cause of mutation or mutation one great cause of hybridity; apparently both views may be in part correct.

Miss Saunders favors a dihybrid scheme for *Petunia,* evidently supposing the difference here also to depend on two complementary factors, both necessary for singleness. Her assumption that singleness is dominant, as in *Matthiola,* seems absolutely untenable. In considering the last point, we may ignore the dihybrid feature, since this evidently concerns only the deviation of the ratio from 50 per cent.

Her formulation, as thus simplified, makes the singles Ss and the doubles necessarily ss; the data then indicate that the functional single pollen is all S-carrying (the reverse of the case in *Matthiola*), since self-pollinated singles produce no doubles. Then, either the single eggs are S + s, and the double pollen s + s, or the single eggs are s + s, and the double pollen S + s. The latter assumption is obviously impossible, since it not only contradicts the assumption that singleness is dominant, but

[9] Theodore Payne, a seedsman of Los Angeles, California, says in his 1914 seed-catalogue, "The weaker seedlings should be carefully saved, as these invariably produce the double flowers."

[10] This is not to assume that some disturbance due to crossing of two single-flowering forms might not have led to the "mutation."

makes both singles and doubles heterozygous (Ss);[11] the former assumption, however, is also excluded, as Miss Saunders shows, by the fact that all singles tested produce some doubles when pollinated by doubles—that is, the expected class of pure singles (SS) does not occur. Evidently, as both Goldschmidt (1913) and Belling (1915) assume,[12] *doubleness* is dominant in *Petunia,* and selective viability probably completes the explanation.

BIBLIOGRAPHY

Bateson, William.

1909. Mendel's Principles of Heredity. 14 + 396 pp. Cambridge, Univ. Press. 6 pl. and 37 fig.

1914. The Address of the President of the British Association for the Advancement of Science. [Heredity.] I. *Science,* N. S., **40**: 287–302.

Bateson, William, and Punnett, R. C.

1911. On Gametic Series Involving Reduplication of Certain Terms. *Jour. of Genetics,* **1**: 293–302, 1 pl. and 1 fig.

Belling, John.

1915. On the Time of Segregation of Genetic Factors in Plants. AM. NAT., **49**: 125–126, Bibliog.

1915a. Conditions of Mendelian Inheritance. *Jour. of Heredity,* **6**: 108.

East, Edward M.

1915. The Phenomenon of Self-sterility. AM. NAT., **49**: 76–87, Bibliog.

Francis, Myrtle Shepherd.

1913. A New Creation in Floriculture. *The Rural Californian,* **37**: 397–399, 410, 411.

[11] In the dihybrid scheme, here, if linkage is to be invoked, as in *Matthiola,* to explain the deviation from 50 per cent. of doubles, both the singles and the doubles must carry *both factors*—since the singles possess both by hypothesis, and we are supposing the pollen of the doubles to show linkage! Further, doubles, not singles, would be expected to be in excess of 50 per cent. In fact, no self-consistent dihibrid scheme seems to be possible with *Petunia.*

[12] Goldschmidt's statement (1913, p. 84) seems to suggest that Miss Saunders herself made this change, especially as he refers to "*Journal of Genetics,* **1**, 1911"; apparently, however, he intends the original article, published in 1910, and I have failed to find any reference to the matter in the part of the volume published in 1911. The explanation given above was stated in a letter sent to her in May, 1914, but no reply has been received. Bateson (1913) considers singleness to be dominant, admitting the necessary conclusion that all cultivated singles appear to be heterozygous. How this universal heterozygosity could be maintained in self-pollination of the singles (S + s eggs × S pollen, since the opposite assumption is untenable), he does not explain.

Frost, Howard B.

1911. Variation as Related to the Temperature-environment. Am. Breed. Assoc. Rept., **6**: 384–395, 4 tables, 4 charts.

[In Ms.] The Relation of Temperature to Variation in *Matthiola.*

[In Ms.] Mutation in *Matthiola.*

Goldschmidt, Richard.

1913. Der Vererbungmodus der gefüllten Levkojenrassen als Fall geschlechtbegrenzter Vererbung. *Zeitsch. f. indukt. Abstam.- u. Vererbungsl.*, **10**: 74–98. Diagr.

Saunders, Edith R.

1910. Studies in the Inheritance of Doubleness in Flowers. I. Petunia. *Jour. of Genetics*, **1**: 57–69, 5 tables, 6 fig.

1911. Further Experiments on the Inheritance of Doubleness and Other Characters in Stocks. *Jour. of Genetics*, **1**: 303–376, 8 tables.

1913. On the Mode of Inheritance of Certain Characters in Double-throwing Stocks. A Reply. *Zeitsch. f. indukt. Abstam.- u. Vererbungsl.*, **10**: 297–310.

Tschermak, Erich von.

1912. Bastardierungsversuche an Levkojen, Erbsen und Bohnen mit Rücksicht auf die Faktorenlehre. *Zeitsch. f. indukt. Abstam.- u. Vererbungsl.*, **7**: 81–234, tables.

de Vries, Hugo.

1906. Species and Varieties: Their Origin by Mutation. 2d ed., 18 + 847 pp. Chicago, Open Court Pub. Co.

THE COAL MEASURES AMPHIBIA AND THE CROSSOPTERYGIA

DR. ROY L. MOODIE

DEPARTMENT OF ANATOMY, UNIVERSITY OF ILLINOIS, CHICAGO

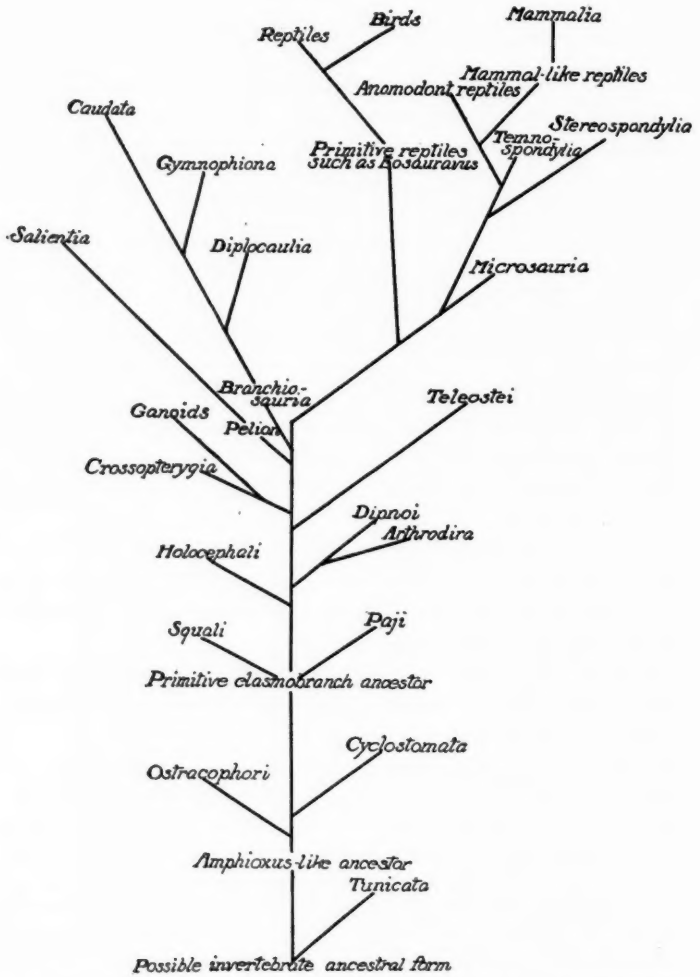
IT has been assumed for many years that the crossopterygian ganoids are more nearly in the direct line of descent of the amphibia than any other known group of fishes. Recent work along this line adds considerable evidence to support this assumption and it is fast becoming accepted as practically proven that such was the line of descent of this group of vertebrates. Watson (1), Broom (2), Gregory (3–4), Pollard (5), Klaatsch (6), Budgett (7), the writer (8), and others have added to our knowledge of this relationship, which is based on the structure of the skull, the limbs and the mandible, so far as these anatomical features are known. Our knowledge of the osteology of neither group is satisfactory and it is to be hoped that additional material will do much toward a solution of this problem.

It is our purpose here to state in a brief manner what the Amphibia from the Coal Measures add toward the solution of the problem of the derivation of the amphibians from the crossopterygians.

The fish characters of the larval stages of the Amphibia have been often cited as evidence of this relationship. Budgett (7) says:

> It has been admitted by the most competent paleontologists that the structure of the dermal bones of the head and shoulder girdle of *Polypterus* is so like that of certain *Stegocephali,* that it must be regarded as more than a mere resemblance while there are many points in the development of the skeleton that distinctly approach the condition of the Amphibia. The only possible interpretation of these facts appears to me to be that the living crossopterygians form a central group among recent forms, having some characters in common with most of the great groups.

The writer (8) has called attention to the similarity of arrangement of the lateral line canals in Amphibia and Crossopterygia and has attempted a correlation of the cranial elements. In that essay it is stated:



A phylogenetic scheme illustrating in a tentative way the possible relationships of the Coal Measures Amphibia to the other Chordata. The Crossopterygia may have had more immediate ancestral relations than the diagram idicates.

The following elements of the stegocephalan cranium are homologous with the same elements in (the crossopterygian) fishes: premaxillæ, maxillæ, nasals, frontals, prefontals, parietals, squamosals, and postfrontals. The epiotics and supraoccipitals of the Stegocephala are homologous with the supratemporal elements of fishes. The quadratojugal is homologous with the subopercular of fishes. The supratemporal is homologous with the preoperculum (8).

Wilder has commented on the close relationship of these two groups and even goes so far as to say: "that terrestrial vertebrates were originally derived from a single form, perhaps a single species" (*i. e.*, of the Crossopterygia) (9). It will be interesting in this connection to give a brief résumé of the geological history of the two groups of vertebrates. The history of the Amphibia is briefly this:

Devonian: *Thinopus antiquus* Marsh, footprint from Pennsylvania.

Mississippian: Footprints from eastern North America.

Pennsylvanian: Five orders of Amphibians represented by hundreds of more or less complete skeletons from Europe and North America.

Permian: Four orders of Amphibia, known from an abundance of material from Europe, Africa, Asia, and North America.

Triassic: Two orders of Amphibia, the species of which may be compared very favorably with modern species; North America and Europe.

Comanchean: None known in North America.

Cretaceous: Caudata known from imperfect fragments, North America.

Eocene to Recent: Frogs and salamanders as in modern times.

Recent: Salientia, Caudata, *Gymnophiona.*

The geological history of the Crossopterygia is briefly summarized by Huxley[1] in the following:

The group of Crossopterygidæ as thus established appears to me to have many remarkable and interesting zoological and paleontological relations. Of the six families which compose it, four are not only Paleozoic, but are, some exclusively and all chiefly, confined to rocks of

[1] Scientific Memoirs, II, p. 445.

the Devonian age,—an epoch in which, so far as our present knowledge goes, no fish belonging to the suborders Amiadæ or Lepidosteidæ (unless *Cheirolepis* is one of the latter) makes its appearance. Rapidly diminishing in numbers the Crossopterygidæ seem to have had several representatives during the Carboniferous epoch, but after this period . . . they are continued through the Mesozoic age only by a thin, though continuous line of Cœlacanthini, and terminate, at the present day, in the two or three known species of the single genus *Polypterus*, now recognized under two genera: *Polypterus* and *Erpetoichthys* (*Calamoichthys*).

Such, in brief, is the geological history of this peculiar order of fishes. At the time of the publication of Huxley's essay the fact of the geological distribution of the group was of the greatest interest, since it proved the transition of a vertebrate group from the Paleozoic to later times in practically unchanged form.

It will thus be seen that in the Devonian we have representatives of these two groups; one of which has been supposed to have given origin to the other. The oldest known Crossopterygian coexisted, in the Devonian, with well-developed Amphibia-like forms if we may trust the evidence of the single imprint of *Thinopus antiquus* Marsh from the Devonian of Pennsylvania. That the impression described by Professor Marsh is in reality a footprint no one, who consults his figures, can doubt. Its geological horizon is vouched for by the late Dr. Charles E. Beecher, whose interpretations of geological facts have never been impeached. So that we may say with perfect assurance that the *oldest known Crossopterygia existed side by side, geologically, with well-developed air-breathing, quadrupedal vertebrates.* Whether the latter were Amphibia or not is a matter which no one, in the light of our present knowledge, can decide. The inference, however, is that they were such.

In order that all the facts of the case in regard to the origin of the Amphibia may be given, the following definition of Crossopterygia is given. It is based on the first definition by Huxley and the definition contained in Zittel's "Paleontology" (ed. by Eastman).

Dorsal fins two, or if single multifid and very long; the pectoral and usually the ventral fins lobate; no branchiostegal rays, but two prin-

cipal with sometimes lateral and median jugular plates situated between the rami of the mandibles; caudal fin diphycercal or heterocercal; scales cycloid or rhomboid, smooth or sculptured.

These characters may be supplemented by the following: Notochord persistent or vertebræ slightly ossified, infraclavicle present. Teeth dendritic in a few forms.

The following list contains brief statements concerning the structures in these two groups which are usually regarded as of great taxonomic importance in all vertebrates.

4. Comparative Table of Structures in Amphibia and Crossopterygia

Amphibia	*Crossopterygia*
I. Typically quadrupedal tetra- and pentadactyl, aquatic or terrestrial vertebrates. Body usually provided with ventral armor of ossified, calcified or chondrified myocommata, present in modern species as strands of connective tissue. Body completely scaled in one species. Scales present in other species but incompletely known.	Aquatic, fring-fined, completely scaled, fishes with dorsal, ventral and caudal fins.
II. Teeth labyrinthine in some species.	Dentine of the teeth dendritic in a few forms.
III. Vertebræ always ossified, sometimes highly developed; assuming various forms. Notochord incompletely persistent as intercentral masses.	Vertebræ usually unossified or incompletely. Notochord largely persistent and but slightly constricted.
IV. Skull covered with dermal bones, which are at times variously sculptured and grooved by pits and canals.	Skull covered by dermal bones which are seldom sculptured although possessing a similar type of lateral line system contained within the skin.
V. Lateral line canals present as distinct impressions in the dermal elements.	Lateral line canals not always impressions in bones, but similar in arrangement to the Amphibia.
VI. Parasphenoid largely developed.	Parasphenoid largely developed.
VII. The following cranial elements correlated with those of the Crossopterygia: Supraoccipital, epiotic, parietal, frontal, prefrontal, nasal, premaxilla, maxilla,	The following elements absent in Amphibia but present in the Crossopterygia: Supratemporal ossicles, ethmoid, hyomandibular, jugular plates, opercular apparatus consisting of operculum and subopereulum.
	Pineal opening present in at least one genus.
	Air bladder present, with at times calcified walls.
	Pelvic girdle composed of rhomboid plate of two parts which may correspond to the ilia.

squamosal, quadrate, pterygoid, palantine, supratemporal, parasphenoid, postorbital. Ethmoid present in Gymnophiona.

VIII. Pineal opening present in most extinct species.

X. No air bladder. Lung anlagen on ventral surface of pharynx.

XI. Pelvic girdle composed of osseous ilium, ischium and cartilaginous or osseous pubis.

XII. Arm consisting of humerus, radius, ulna, carpals (sometimes cartilaginous), metacarpals and phalanges.

XIII. Leg composed of femur, tibia, fibula, tarsus (sometimes cartilaginous), metatarsus and phalanges.

XIV. Ribs single, long or short, heavy or slender, inter- or intracentral.

XV. Form of body not fish-like.

XVI. Mesonephros functional in adult.

XVII. External gills slender and thread-like in the young of all living and some of the ancient forms.

Pectoral fin composed of pro-, meta—, and mesopterygium, actinosts and fin rays. Broom (2) has correlated the elements in the arm of *Sauripteris taylori* with those of the amphibian arm down to the actinosts, which he regards as carpals. The fin rays would represent phalanges.

Pelvic fin composed of basiost which represents the femur, and meta- and mesoptergyia and fin rays.

Ribs double; dorsal, arising independently of transverse processes; ventral one an exogenous process of vertebra, which in the tail becomes the hæmal arches by fusion of the tips.

Form of body always typically fish-like.

Mesonephros functional in adult.

External gills of young, slender, thread-like, recalling those of larval salamander.

It will be seen from the above list of comparative structures that there are a variety of instances in which the two groups approach each other. It is, however, to be clearly kept in mind that the oldest known Amphibia, as indicated by our present knowledge of these forms, are more like the modern forms of Amphibia than they are like the ancient types of fishes from which they supposedly have been derived. In other words, a more complete knowledge of the Coal Measures Amphibia has not served to simplify our ideas of amphibian descent in the least, but rather to confuse them.

All of the early Amphibia have well-developed ambulatory or natatory limbs and none of them are fish-like in

external form. Many of the representatives of the Amphibia in the Coal Measures of North America are highly specialized and adapted for a variety of modes of life. One of the most significant factors in the derivation of the early land vertebrates from the fishes is the question of the origin of limbs from fins, on which much has been written from a theoretical standpoint, but nothing has been seen in the nature of material supporting and defining the details in the process of evolution. It must be remembered, however, that the Coal Measure forms are Amphibia in a high stage of development and when new discoveries show us the anatomy of the forms from the Mississippian, Devonian and possibly the Silurian, then we shall be in better shape to discuss the question of the origin of tetra- and pentadactyl limbs.

The evolutional status of the Coal Measures Amphibia may be briefly stated. They were an assemblage of forms, highly developed and highly specialized, with few primitive characters which would tend to ally them directly with any known group of more primitive vertebrates. We should expect to find among these Paleozoic Amphibia some evidence of a transitional type of limb (11) structure between that of *Eusthenopteron* (12), or allied Crossopterygian, on the one hand, and the pentadactyl terrestrial vertebrate, on the other. But such evidence is not forthcoming among the material at present available. Evolutional forces had brought about a wide diversion of faunas in the Coal Measures, so that the species are easily separable into distinct geographic groups, which are more distinct than are the species of Amphibia inhabiting the same regions to-day.

The living Amphibia are much more commonly identical in eastern Ohio and northern Illinois than were the species of the same order during the Coal Measures. Species of *Necturus, Amblystoma, Rana* and *Bufo* are not widely different in the two localities referred to; yet the species of Amphibia during the Coal Measures at Mazon Creek, Illinois, and Linton, Ohio, are widely distinct. They are, in fact, more widely distinct than the species of

modern Amphibia existing in New York and in California; for in these states we find modern genera in common. This wide diversion of structure between the faunas of Linton and Mazon Creek is not due to difference in age, since it is almost assured that they were nearly contemporaneous geologically.

The high degree of specialization attained by various members of the Coal Measures Amphibia is remarkable. They had become adapted to nearly every condition of vertebrate existence, which animals of later times have adopted. There were strictly aquatic, fossorial, terrestrial, climbing, crawling, worm-like, snake-like, lizard-like, crocodile-like, all living contemporaneously. The absence of fish-like forms is noteworthy.

1. Watson, D. M. S. 1912. The Larger Coal Measure Amphibia. *Mem. and Proc. Manchester Lit. and Philos. Soc.*, LVII, No. 1, pp. 1–4, 1 pl.
2. Broom, R. 1913. On the Structure of the Mandible in the Stegocephalia. *Anat. Anz.*, Bd. 45, No. 2/3, pp. 73–78, figs.
3. Gregory, W. K. 1911. The Limbs of *Eryops* and the Origin of Paired Limbs from Fins. *Science*, N. S., 33, No. 848, pp. 508–9.
4. Gregory, W. K. 1913. The Crossopterygian Ancestry of the Amphibia. *Science*, N. S., 37, No. 960, pp. 806–8.
5. Pollard, H. B. 1891. On the Anatomy and Phylogenetic Position of *Polypterus*. *Anat. Anz.*, Bd. VI, p. 338; *Zool. Jahrb.* (Morphol. Abth.), V, 1893, pp. 387–428, with pl.
6. Klaatsch. Hermann. 1896. Die Brustflosse der Crossoptyeygiaer. *Festschr. für Gegenbaur*, Bd. I, pp. 259–391, Taf. I–IV.
7. Budgett, J. S. 1902. On the Structure of the Larval Polypterus. *Trans. Zool. Soc.*, London, XVI, Pt. VII, October; Works, pp. 154–176, pls. X–XIII, 1907.
8. Moodie, R. L. 1908. The Lateral Line System in Extinct Amphibia. *Journ. Morph.*, XIX, No. 2, 511–540, 17 figs.
9. Wilder, H. H. 1909. History of the Human Body. New York, Henry Holt and Co. Amphibia, pp. 541–2.
10. Moodie, R. L. 1915. The Scaled Amphibia of the Coal Measures. *Science*, N. S., Vol. XLI, No. 1056, pp. 463–464, 1915.
11. Gregory, W. K. 1913. Crossopterygian Ancestry of the Amphibia. *Science*, N. S., XXXVII, No. 960, pp. 806–808.
12. Patten, Wm. 1912. Evolution of the Vertebrates and their Kin, p. 391, Fig. 265.

SHORTER ARTICLES AND DISCUSSION

AN ANTICIPATORY MUTATIONIST

WHENEVER any new view gains acceptance it is usually found to have been partially anticipated in the writings of various authors. The mutation theory is no exception to this rule, and the purpose of this note is to direct wider attention to the anticipation of mutationist views by Thomas Meehan. While it is known to some that Meehan held such views, it is not, I think, generally realized how consistently and persistently he advocated them throughout the course of his life.

Thomas Meehan was born near London in 1826, was trained as a gardener at Kew and afterwards came to America. He settled in Philadelphia as a horticulturist, became a prolific writer for agricultural and horticultural journals and finally, in 1891, established *Meehan's Monthly,* a journal devoted to gardening. He traveled as far as the Rocky Mountains and Alaska, was appointed state botanist for Pennsylvania, and was in 1875 elected a fellow of the American Association for the Advancement of Science. His publications included "Native Flowers and Ferns of the United States," in four volumes, and the current of his work continued until after his death in November, 1901.

But the phases of his active life which I wish to emphasize here were (1) his keenness and accuracy as an observer, and (2) his constant advocacy of discontinuity in the variations of species on the basis of his own observations, at a time when such views were by no means popular. Meehan was particularly active in the Philadelphia Academy of Science, and he contributed in all no less than 257 papers and notes to the *Proceedings* of that society between the years 1862 and 1901.

Although Meehan accepted evolution with his contemporaries and with Darwin, yet he never lost an opportunity to emphasize the probable significance of the wide variations which he frequently observed in nature, as opposed to the insensible changes which were believed to furnish the material for evolution. The character of his observations as well as the trend of his views, may be indicated by a few quotations from his writings.

In a paper entitled "Change by Gradual Modification not the Universal Law,"[1] he begins as follows:

Natura non facit saltum has been accepted as a grand canon by most naturalists, and the evident absence of connecting links has been thought fatal to theories of evolution. My studies in plant life lead me to the belief that one form will spring from another essentially different, and without any gradual or insensible modifications uniting them.

He then describes a variation in *Halesia tetraptera*.[2] The new form had undergone a change in leaf shape and the veins were rugose. The flowers, instead of having a narrow tube at the base, were open, cup-shaped, the pistil wholly enclosed and not exserted. This form produced good seeds and if found wild would be considered a new species.[3] He then refers to a variation in *Yucca filamentosa*. One plant in hundreds threw out a more branching panicle which opened two weeks earlier. Its characters remained and were continued in the progeny. After citing other cases, Meehan says:

Not only do strikingly distinct forms come suddenly into existence but once born they reproduce themselves from seed, and act in every respect as acknowledged species.

He states that a "weeping" variety of the peach came into existence "about 30 years ago," and also "ten years ago a deep blood-leaved variety appeared." The following quotations from the same paper will serve further to illustrate his views:

In over a quarter of a century of experience among living plants, I have rarely known any striking form to have originated by gradual modification, but always by one great leap. The slight changes are generally in efforts backwards; as when we sow purple beech seed, some few are a trifle paler than their parents; there is little or no hesitation in the forward leap. . . .

Forms are not only called into existence suddenly, widely different from their parents, and can reproduce themselves from seed, but they come into existence without seed agency, and the same or similar form in widely separated localities, and not all necessarily by seed from one individual.

Flowers of *Viola pedata* were sent to him from five localities in Pennsylvania, New York, Illinois and Indiana, having "the two upper petals a beautiful maroon color as in the pansy."

[1] *Proc. Amer. Assoc. Adv. Sci.*, 1874, B. 7–12, 1875.

[2] Now known as *Halesia carolina* L.

[3] This fuller account is taken from his later paper, "Variation in *Halesia*," *Proc. Phila. Acad.*, 1884, 32–33, Figs. 4, 1885.

Among the conclusions of this paper, which pretty well sums up his views, we find,

> Morphological changes in individual plants are by no means by gradual modification,

and

> New and widely distinct species may be suddenly evolved from pre-existing forms without the intervention of connecting links.

A discussion followed in which Professor Morse, C. V. Riley, Professor Gill and Asa Gray took part, but although some agreed that there was no reason why marked changes and gradual modifications should not both play a part in evolution, yet the tendency was rather to look upon the former as sports which were of little evolutionary significance. Meehan afterwards referred to this paper as showing that:

> New forms "jumped" into existence, and frequently these new forms were diverse from each other, under precisely the same "environment" as far as human knowledge had yet reached, as had been the surrounding circumstances of the parent form.

Quotations of a few of Meehan's other papers, with notes upon them, will serve to show the range of his ideas and the accuracy of his observations.

"On the Agency of Insects in Obstructing Evolution," *Proc. Phila. Acad.*, 1872, 235–37, 1872.

"On Rapid Changes in the History of Species." *Proc. Phila. Acad.*, 1884, 142–43, 1885.

"Persistence in Variations Suddenly Introduced," *Proc. Phila. Acad.*, 1885, 116, 1886.

> We see that identical forms may appear simultaneously in localities widely separated; and, the circles meeting, cover a district in a comparatively short time.

"Spicate Inflorescence in *Cypripedium insigne*," *Proc. Phila. Acad.*, 1885, 30–32, 1886.

> Such a belief [in jumps] would tend materially to remove difficulties in the way of theories of evolution, that now prevented a full acceptance thereof.

"On a White-seeded Variety of the Honey Locust," *Proc. Phila. Acad.*, 1885, 404, 1886.

In this paper he describes a tree of *Gleditschia triacanthos* growing near Germantown, Pa., which had seeds white instead of dark olive-brown. They also differed in shape, being nearly

orbicular, instead of narrowly ovate, and twice as long as broad. He remarks in this paper:

> When variations occur it is difficult for some to believe that cross-fertilization, a return to some characteristic of an ancient parent, or some accident of climate or soil had not [been] an agency in the change.

This type of difficulty is still formidable in the minds of some. In the case he describes such explanations are excluded as inapplicable.

"On Parallelism in Distinct Lines of Evolution," *Proc. Phila. Acad.*, 1886, 294–95, 1887.

Meehan refers[4] to a paper given by him at the Troy meeting of the American Association (1870), "On the Introduction of Species by Sudden Leaps." But there is no such paper in the report, although he gave three other papers dealing respectively with fasciation, pollination by insects, and the influence of nutrition on sex. His last paper, published posthumously, in *Proc. Phila. Acad.*, 54, 33–36 (1902), is in two parts, dealing with "The Bartram Oak, in Connection with Variation and Hybridism" and "Observations on the Flowering of *Lobelia cardinalis* and *Lobelia syphilitica*." He may well be described with justice and accuracy as an anticipator of the mutation theory, not on theoretical grounds but on the basis of his own keen observations.

Meehan also contributed to the earlier volumes of the AMERICAN NATURALIST, the *Botanical Gazette*, *Torrey Bulletin* and other journals during his active life. One of these[5] characteristically sets forth his mutationist views.

R. RUGGLES GATES

[4] *Proc. Phila. Acad.*, 1885, 30.

[5] On the Relation Between Insects and the Forms and Character of Flowers," *Bot. Gazette*, 16, 176–77, 1891.